# IMPROVEMENT OF
FLOWERS BY BREEDING

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AGRICULTURE is above all things practical, and probably few people would think of it as concerned with the production of sheer beauty. Yet American agriculture has $290,000,000 invested in producing beauty, and it pays to the extent of a gross return of $131,000,000
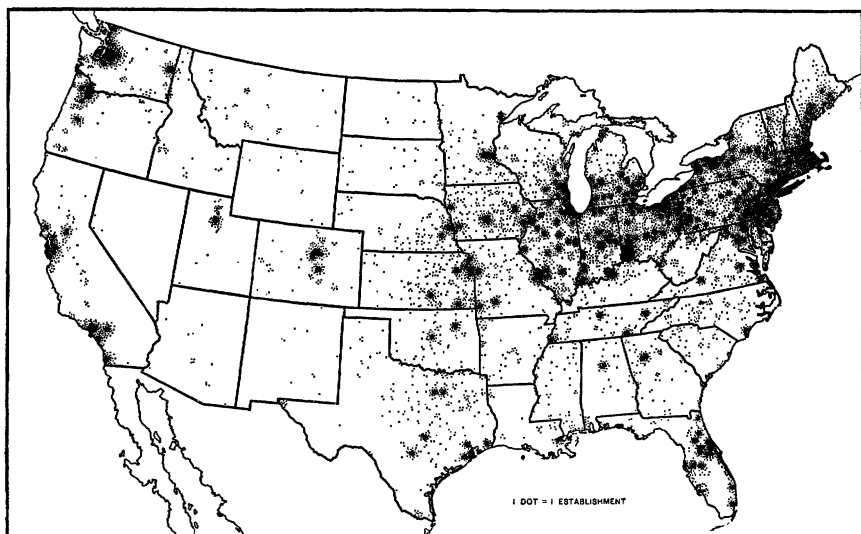
Figure 1.—Approximate location of florists' establishments producing flowers and plants grown under glass and flowers grown in the open, 1929.

a year. These figures apply to the farms and nurseries engaged in growing flowers and ornamental plants, outdoors and under glass.[1] The map (fig. 1) shows both how widespread the industry is and how heavily it is concentrated in certain regions.

This great industry supplies material for the immense number of people who grow flowering and ornamental plants for their own enjoyment. During recent years there has been a rapid increase in the

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[1] In 1929, according to the census, there were 13,088 florists producing flowers and plants as a business, both under glass and in the open. The number of commercial nurseries at that time was 7,207, and probably most of these devoted at least part of their space and time to the production of ornamental plants. In addition, 1,935 farms were reported as engaged in growing bulbs commercially. The number of farms engaged in producing seed of flowering plants—a well-developed industry on the Pacific coast, expecially in California—was not included.

planting of flowers around homes and in the planned planting of streets, roadways, and parks. The large number of flower shows and exhibits, ranging from the small display of a village garden club to the huge annual national and international shows, is one evidence of this interest. In some of these shows the competition for prizes for new or improved strains or seedlings has become very intense, especially among fanciers of one kind of flower, such as the chrysanthemum, dahlia, gladiolus, rose, or iris.

These demands of both florists and home growers have been the major influence in the development of new and finer types of flowers, and each year there are many new introductions. Undoubtedly changing fashions play a large part in this activity, and the florist must be constantly on the alert to meet them.

BACKGROUND OF FLOWER BREEDING

IT IS likely that our early ancestors were too busy securing the bare necessities of life to pay much attention to plants that had nothing but their beauty to recommend them. Conscious selection of purely decorative plants probably did not begin until some sort of stable living conditions had been achieved. When early man first began to grow flowers, he very likely transplanted entire clumps from the wild to his dooryard. It is only natural that he should have chosen the best for transplanting and thus practiced the first plant selection in ornamentals. As time went on, the use of flowers and ornamental plants played an ever-increasing part in his everyday life. We know from the remnants of early art that flowers were regarded highly, since so many of them furnished the chief motif in decoration.

The early records of selections and attempts to breed flowering plants are very meager. Considerable work had undoubtedly been done by the beginning of the eighteenth century. The first apparently authentic record of hybridizing flowers, however, appeared in 1717, when Thomas Fairchild's cross between a carnation and a sweet-william was reported. This occurred during a period when considerable interest had been aroused by the work of Camerarius, who demonstrated the existence of sex in plants.

The species hybrid produced by Fairchild was completely sterile and was commonly referred to as the plant mule. The chief interest of the botanists of this period was not so much the production of better plants as the accumulation of evidence on sexuality in the plant kingdom. Fairchild's hybrid, however, received considerable attention and was described in 1717 in Bradley's New Improvements in Planting and Gardening, as being neither sweet-william nor carnation, but as resembling both equally.

WORK OF AMATEUR AND PROFESSIONAL BREEDERS

After the existence of sex in plants had been generally accepted, it is probable that countless amateurs carried on some sort of breeding work with flowers. The development of many new varieties and strains during the nineteenth century indicates the wide interest in this type of work. Even at the present time many of the new and improved types of flowers are being produced by amateur breeders. The work of the amateur is frequently done on a very small scale in

a back-yard garden. In the numerous organizations interested in some one flower, such as the American Rose Society, the American Iris Society, and others, there are many members engaged in the fascinating hobby of flower breeding. A great deal of this work is never heard of, but undoubtedly it has produced many of our present varieties of such important flowers as iris, gladiolus, dahlia, rose, and narcissus. It involves the making of many thousands of crosses each year in a very wide range of plant material. In an article such as this, it is obviously possible to mention the work of only a few amateur breeders, and this is done here and there under sections dealing with particular plants. It is likewise not possible to discuss all the numerous varieties that have been developed by flower breeders. The following résumé of the number of listed varieties of some of the groups of the commoner flowers is evidence of the extent of interest in this field.

Name	Number of varieties
Rose	15, 000
Chrysanthemum	1, 500
Narcissus	3, 000
Tulip	8, 000
Sweet pea	500
Snapdragon	400
Aster	600
Dahlia	7, 000
Gladiolus	2, 500
Iris	·4, 000
Peony	2, 000

Since new varieties are constantly appearing and old ones going out of fashion, the data of this tabulation can be accepted only as approximations. The origin of most varieties of flowers is unknown, and it is beyond the scope of this article to attempt to indicate this for each kind of flowering or ornamental plant, but the named varieties of the plants included in this discussion far exceed in number those of our important food plants. It is safe to say that the production of such a large number has been possible only because of the work of thousands of amateur breeders, whose main compensation has been the pleasure the work has afforded them.

The contributions of the professional breeders, including nurserymen, florists, and seedsmen, are likewise very large. It is to the work of this group that we owe the development of nearly all our modern varieties of such important flowers as the rose, zinnia, sweet pea, carnation, calendula, aster, snapdragon, larkspur, and nasturtium. While it is true that profit has been a primary factor in this work, the professional breeder almost always has an inborn love for the plants and flowers that are his stock in trade.

Practically all the large flower-seed growers are carrying on extensive breeding programs. Of the many new flowers or so-called novelties introduced to the public each year, some have arisen as recombinations following chance crosses that occurred in the fields in previous years, and a very few may be spontaneous mutants, but most are the result of selections within lines that are mixed or not genetically pure in their ancestry (fig. 2). The opportunity for such selection on a large flower-seed farm is very great. It is not unusual, for

instance, to see as many as 5 acres of some one flower, with as many as 430,000 individual plants. This means that the possibility of finding rare multiple recessives is fairly great. Here it is not a question of following the inheritance of one or a few genes. The trained geneticist has an opportunity to find nearly every combination of characters that could possibly arise from the material (fig. 3).
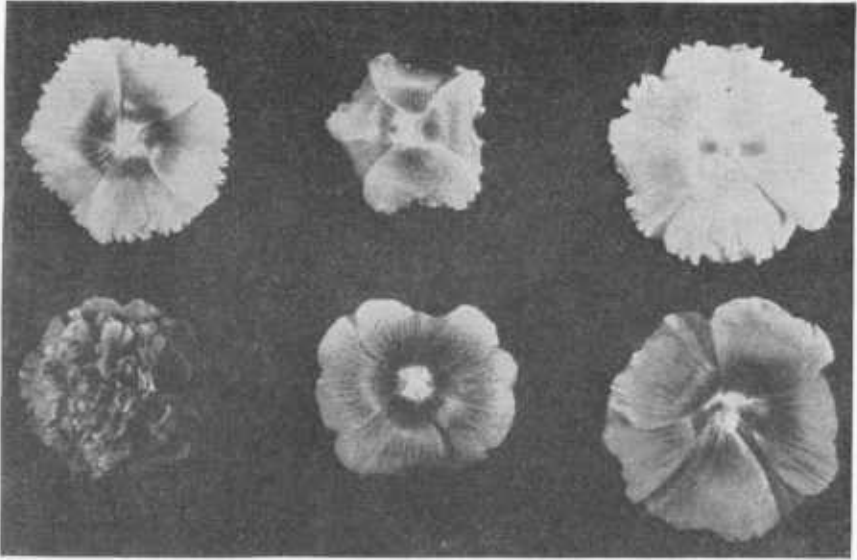

Figure 2.—Variation in hollyhock flowers collected from a group of plants growing in a garden at Davis, Calif. By selection and by controlling pollinations for several years all but the double form could probably be made to breed true. The double shown here is a rather complex form that cannot be bred to come true from seed.

When a new outstanding type appears in a field it is usually recognized. If it seems desirable, a stake is placed beside it and the seed is collected as it matures. In recent years the more careful growers take measures to protect the selected plant against cross-pollination if it is a species not normally self-fertilized (fig. 4). As many as several thousand such field selections may be made each year on a large flower-seed ranch. Only the best variants are carried on, and these are usually not introduced until they breed fairly true to type. While undergoing this period of selection and reselection they are said to be "in the shop" (fig. 5).

There is no doubt that the flower varieties of today are a vast improvement over those of 15 to 20 years ago. Undoubtedly we owe a real debt of gratitude to the amateur and professional breeders whose efforts have made this possible. When it is recalled that most of this work has been accomplished without the aid of a background of knowledge of genetics, the possibilities for the immediate future are indeed bright. In many instances the results could have been accomplished in a much shorter period, and frequently a smaller population of plants would have sufficed. Unfortunately there still

exist many erroneous ideas and beliefs among flower breeders. Some of these will be discussed later in this article.

NEED FOR MORE SCIENTIFIC METHODS

The accumulation of data and the development of fundamental principles in genetics have gone on at a rapid pace during the last 25 years. As a result there is now available sufficient information prac-

Figure 3.—A field planting in California of annual larkspur for seed. There are several hundred thousand plants in a field of this size. To many the plants would appear uniform, but to a trained investigator there would be countless variants as to flower shape, color shades, plant habit, foliage, and many other characters. (Courtesy of Bodger Seeds, Ltd.)

tically to revolutionize the practices of the average amateur and professional flower breeder. Unfortunately this material is not readily accessible, being widely scattered in scientific journals and papers in many different languages.

Much of the unfamiliarity of flower breeders with this mass of information is probably due to the fact that it has never been called to their attention. For instance, geneticists have known for years that the common flowering stocks (*Matthiola incana* (L.) R. Br.) were limited to a maximum of about 56 percent of doubles and that no more can be obtained; yet considerable money is being spent by florists and seedsmen each year to breed strains that will produce a higher proportion.

No one would think of stepping into an airplane and attempting to fly it without some preliminary instruction, yet apparently nearly

everyone thinks the only requisite for success in flower breeding is a liking for the work. If this article seems to be somewhat more technical than the reader might expect, considering the popular appeal of the subject matter, it is because the authors believe the time has come when those interested in improving flowers must be ready to put some effort on studying the basic elements of their science. Planned breed-

ing is unquestionably a fairly complex job. It does not sit and wait for the "breaks" but goes out and makes them. It has its rules and principles, and he who becomes familiar with them is well repaid in increased efficiency. Some of these rules and principles will be discussed in the following pages.

Most of the early technical investigators who worked with flowers were interested mainly in establishing fundamental principles of inheritance. This explains why, until very recently, so few varieties of flowers or ornamentals have been produced by technical workers. Following the rediscovery of Mendel's work in 1900, numerous experiments were carried on to test the validity of his laws. In a goodly share of these, some species of flowering plant was

Figure 4.—A type of bag commonly used to protect selected flower plants from cross-pollination. A stake is driven into the ground close to the plant and a tin or galvanized-iron cylinder open at both ends is placed around the base of the plant and stake. A long cloth bag open at both ends is pulled down over the plant and stake, tied tightly about the metal cylinder, and closed at the top with a drawstring. This gives protection from insect visitors, and if mesh of cloth is fine enough also from wind-blown pollen.

used as experimental material. As a result there was built up a considerable amount of data on the inheritance of many characters in a wide range of flowering plants. This has been summarized and is presented in the appendix of this article.

Recently the possibility of producing strains of flowers resistant to diseases has been receiving more than usual attention. The achievements in this field with some plants such as wheat, sugar beets, cabbage, etc., have stimulated a desire for similar work with flowers. The control of many virus and fungus diseases of flowers is very difficult and offers a challenge to the plant breeder. The success achieved with wilt-resistant asters (fig. 6) and rust-resistant snapdragons is an

indication of the immense possibilities. In this type of work it is very probable that technical workers in public-service institutions will lead the way. A close cooperation between pathologists and geneticists will be essential and is now provided in many experiment stations and in the United States Department of Agriculture. Work in this
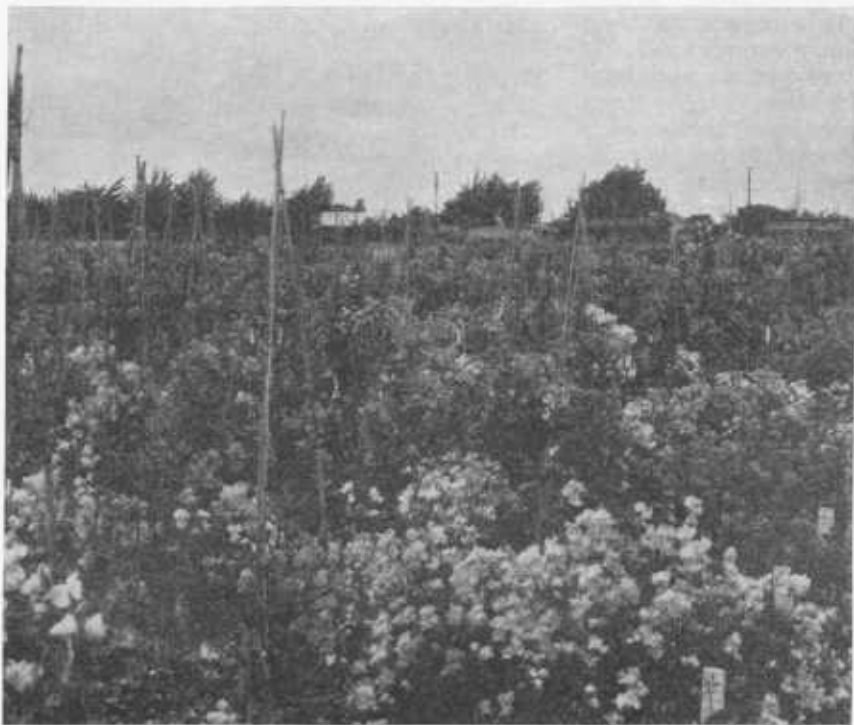
Figure 5.—A sweet pea "workshop" in California. Seed from controlled crosses is planted in rows, and when plants are in bloom the breeder takes notes on each lot, selecting the most desirable for further breeding. Three long bamboo stakes are placed to form a tripod over each selected plant, and if seed is to be saved a little bag is numbered and tied to the bamboo support. (Courtesy of Ferry-Morse Seed Co.)

field may become involved in difficulties, such as the sudden appearance of other forms of a disease-producing organism that are able to infect hitherto resistant plants. These so-called physiological strains of fungi are discussed at some length in the section on wheat in the 1936 Yearbook of Agriculture. They will be mentioned later under the discussion of rust resistance in snapdragons.

There is also a demand for types better suited to certain unfavorable environmental conditions, such as winter cold, drought, or intense heat. At the present time practically all of the breeding work on flowers is restricted to certain sections of the United States and of Europe. It is very probable that some genetic material discarded as undesirable in one region might be extremely valuable if grown under a different set of environmental conditions. For instance, too glaring

colors would very likely be less intense in a warmer, sunnier climate and the washed-out pink of a hot region is apt to be about right in a cooler habitat. Long, slender, weak stems in a warm section are commonly shorter and sturdier when the plants are grown under cooler conditions.

The effect of length of day on blooming is another very important point that is now given scant consideration by the average flower

Figure 6.—Wilt-resistant and susceptible asters planted side by side on infested soil. The susceptible plants on the right have been practically wiped out by the disease. (Courtesy of Bodger Seeds, Ltd.)

breeder. When plants of a species known to be sensitive to day length are selected for blooming at some particular time of year in one latitude, it should be remembered that in another their behavior in this respect is likely to be different.

The breeding of winter-hardy perennials is just now beginning to receive some attention. Here also, results will depend to a considerable extent on the location in which the plants are to be grown. Low atmospheric temperatures are less destructive if there is a heavy blanket of snow. This explains why some flowering perennials overwinter nicely in Canada, but are frequently winter-killed in the Ohio Valley.

A very valuable aid in the breeding of flowers is the collecting of new germ plasm by introducing species and varieties native to other parts of the world. This has been done in this country chiefly by the Division of Plant Exploration and Introduction, of this Bureau. The many botanical gardens in all parts of the world also exchange

seeds and plant materials. While some of these introductions are rather unattractive as measured by American standards, yet they may carry very valuable genes. In many instances these "immigrant genes" can be introduced into some of our own standard varieties, giving new and more desirable strains.

As a result of widespread interest and to stimulate greater effort, American seedsmen have established an annual testing of new flowers in what are called the "All-American Trials." New varieties entered by seed growers are planted at a number of locations scattered over the country. A committee of qualified seedsmen in each region observes these plantings and rates each new production on its merits. Awards are then given for the most outstanding introductions. This plan has afforded an excellent stimulus to flower breeding and has probably had much to do with the recent expansion of this work by seed growers.

TECHNIQUE OF BREEDING

THE first step in breeding work is the transfer of pollen from the anthers to the stigma of a flower. Two types of pollination are distinguished: self-pollination, when the pollen is produced by the same flower as the seed or by another flower on the same plant; and cross-pollination, when the pollen comes from another plant. Self-pollination is easily accomplished in most cases by enclosing the plant or its flowers in some sort of cloth cage or paper bag so as to protect them from all pollen except their own (fig. 7). Some plants may need a pollinating agent, even though they are fully self-fertile, because the pollen of the flower is shed before its own stigma is receptive, or because the stigma protrudes up above the anthers, or for some other reason. Sometimes such plants merely need to be shaken several times each day in order to scatter the pollen in the bag or cloth cage. Sometimes the best pollination can be secured by the aid of insect visitors, such as flies, bees, or some other species [2] introduced into the cage.

Frequently, however, there is difficulty in getting certain crosses to "take." Sometimes the pollen grain is unable to germinate on the stigma; sometimes it germinates but fails to grow down the style to the egg; sometimes it grows down the style, but the rate of growth is too slow to effect fertilization. Some ingenious devices have been used to overcome these difficulties. When the pollen grains refuse to start growth, they may be germinated in a very weak sugar solution, which is then daubed on the stigma. If the difficulty is due to slow rate of growth, the pollen grains may be placed on the stigma of a young, unopened flower so that they have the advantage of an early start on their journey. If the pollen tubes simply cannot grow down the style tissue, however, there seems to be no remedy, though the same pollen may function normally on the stigma of another closely related plant.

Some investigators have thought that the retardation of growth of pollen tubes was a result of some sort of inhibiting material present either in the style or the ovary of the flower. A Japanese scientist,

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[2] See the article on Onion Improvement in this Yearbook for a description of this method.

Yasuda (*558*),[3] became interested in this problem and devised a unique experiment with petunias. In these flowers there occur some self-sterile races. Preliminary work indicated that sterility was due to a slow rate of growth of the pollen tubes. The same pollen applied to other races grew rapidly and effected fertilization. Yasuda conceived the idea of grafting styles from one race of petunias to another. The reader who is familiar with the parts of an average petunia will readily appreciate his difficulties. This very delicate operation was performed with a fairly high degree of success by gluing the grafted style, including its stigma, to the new ovary with a thin layer of gelatine. It was then held in place by being tied, with a thread taken from a spider's web, to a very fine wire support fastened rigidly beside the flower. Since Yasuda wished to determine the source of the material that inhibited the growth of the pollen tubes, he made reciprocal grafts.

After the grafts had "taken", pollen was applied to each stigma. On some stigmas the plant's own pollen was applied; on others, pollen from another race. In each instance ungrafted styles were used

Figure 7.—Controlled pollinations of snapdragons. Flowers are enclosed in a glassine bag, and each operation is recorded on attached tag. (From Hilgardia, University of California.)

as checks, some self-pollinated and some crossed. The rate of growth of pollen tubes from the plant's own pollen was more rapid in its own styles when they were grafted on ovaries of another race. Yasuda thought this indicated that an inhibiting substance might originate in the ovary of the flower. Unfortunately, though the rate of pollen-tube growth was given, no statement was made as to whether seed was actually set in ovaries with grafted styles. In this work Yasuda was interested only in the possible presence of the inhibiting material that caused a slow rate of pollen-tube growth.

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[3] Italic numbers in parentheses refer to Literature Cited. See notice, p. 977.
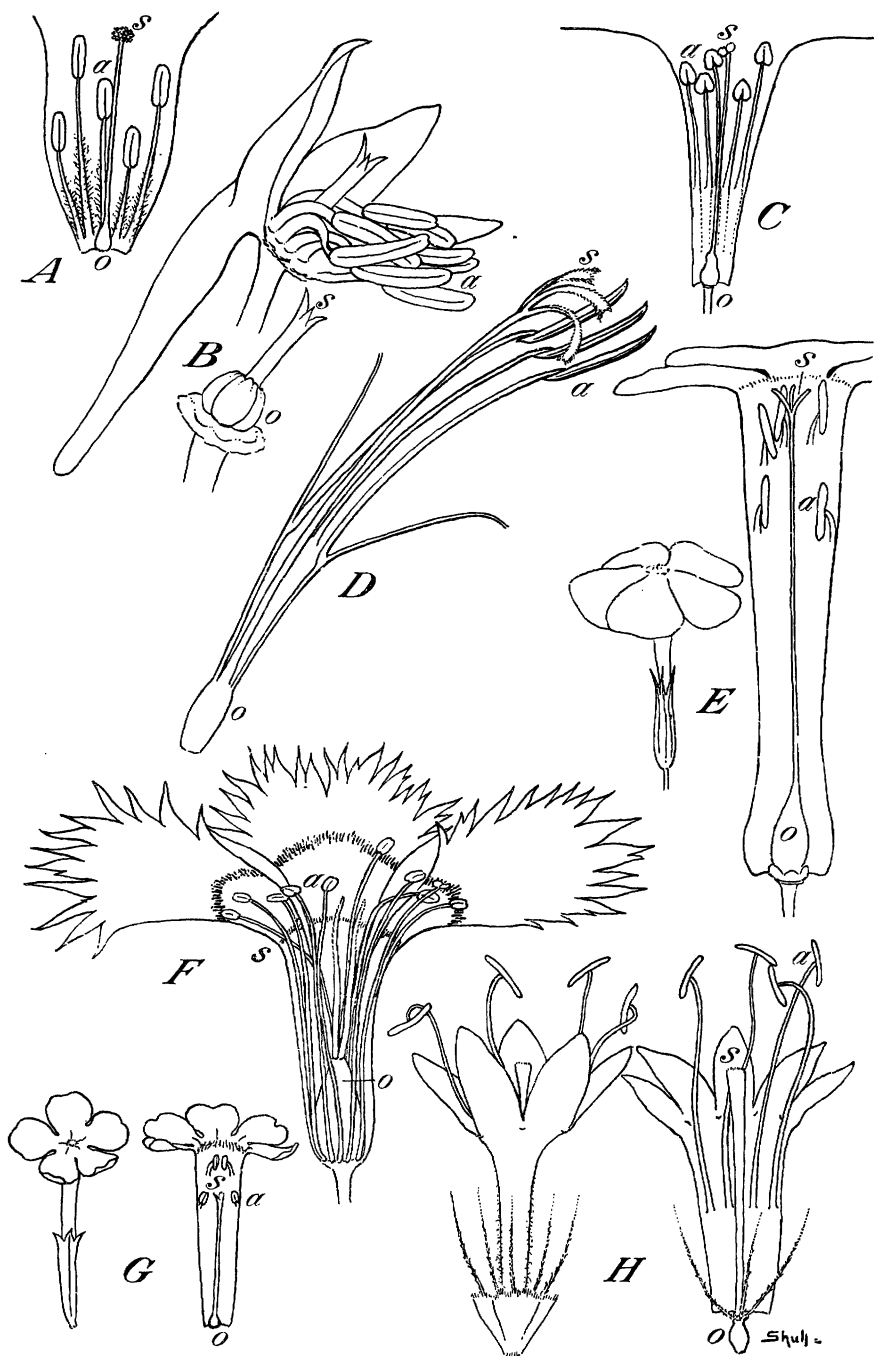
Figure 8.
(Legend on opposite page.)

This same condition of retarded growth rate of pollen tubes is also known in other plants. It has been shown in tobacco and a few others that a series of genes actually control pollen-tube growth, and it is assumed that such genes cause the formation of these inhibiting materials.

The unique method of Yasuda may lead to something valuable in flower breeding. In some cases of cross-pollination where the pollen will not grow in the maternal style it may be possible to secure hybrids by grafting a style from the pollen parent to the seed parent. This, of course, would not work if the inhibiting cause is a substance in the maternal ovary.

Successful cross-pollination depends to a great extent on having a thorough knowledge of the structure of the flower to be pollinated. In some instances it may be so constructed that considerable skill in manipulation is necessary to secure even a low percentage of successful crosses.

When a cross-pollination is to be made it is essential that every precaution be taken to safeguard the stigma from all other pollen. In general this requires the removal of the anthers before pollen is shed. In the case of many members of the composite family, such as marigolds, this is so difficult that another less certain but fairly efficient method is sometimes used. It is based on the structure of the composite floret, in which the style is surrounded by the anthers, which form a closed circle about it. As the style grows it pushes up through the column of anthers, collecting pollen as it goes. The rate of this growth is so rapid in some composite flowers that the stigma emerges from the anthers before the pollen has had time to germinate. If a fine stream of water of moderate force is used promptly, the pollen grains can frequently be washed from the stigma before they germinate.

The structure of some of the commoner flowers is shown in figures 8, 9, and 10. In each instance a longitudinal section is shown in order to bring out clearly the floral parts most important in pollination— the anther, the stigma, and the ovary.

Figure 8 shows some of the flowers in which controlled pollination is most easily effected.

The morning-glory (fig. 8, *A*) is an easy type of flower to emasculate. As shown in the drawing, the style is slightly longer than the stamens. Such a style is said to be exserted beyond the anthers. When a cross-pollination of morning-glories is to be performed, the anthers are removed at any time before they shed their pollen.

The petunia flower shown in figure 8, *C,* is very similar to the morning-glory. There are, however, other flower types in petunia that are more complex. In some of the extreme double types the stamens are greatly reduced or eliminated entirely. Such a flower can be used only as a maternal parent, and crosses are easily made since anthers are not present.

Figure 8.—Structure of (*A*) morning-glory, (*B*) nasturtium, (*C*) petunia, (*D*) gladiolus, (*E*) phlox, (*F*) carnation, (*G*) verbena, and (*H*) scabiosa to show arrangement of the parts concerned in pollination. The anthers, stigma, and ovary are labeled *a, s,* and *o,* and in all instances each flower has been split open and drawn to show the relative position of these three parts. The technique for pollination of each is discussed in the text.
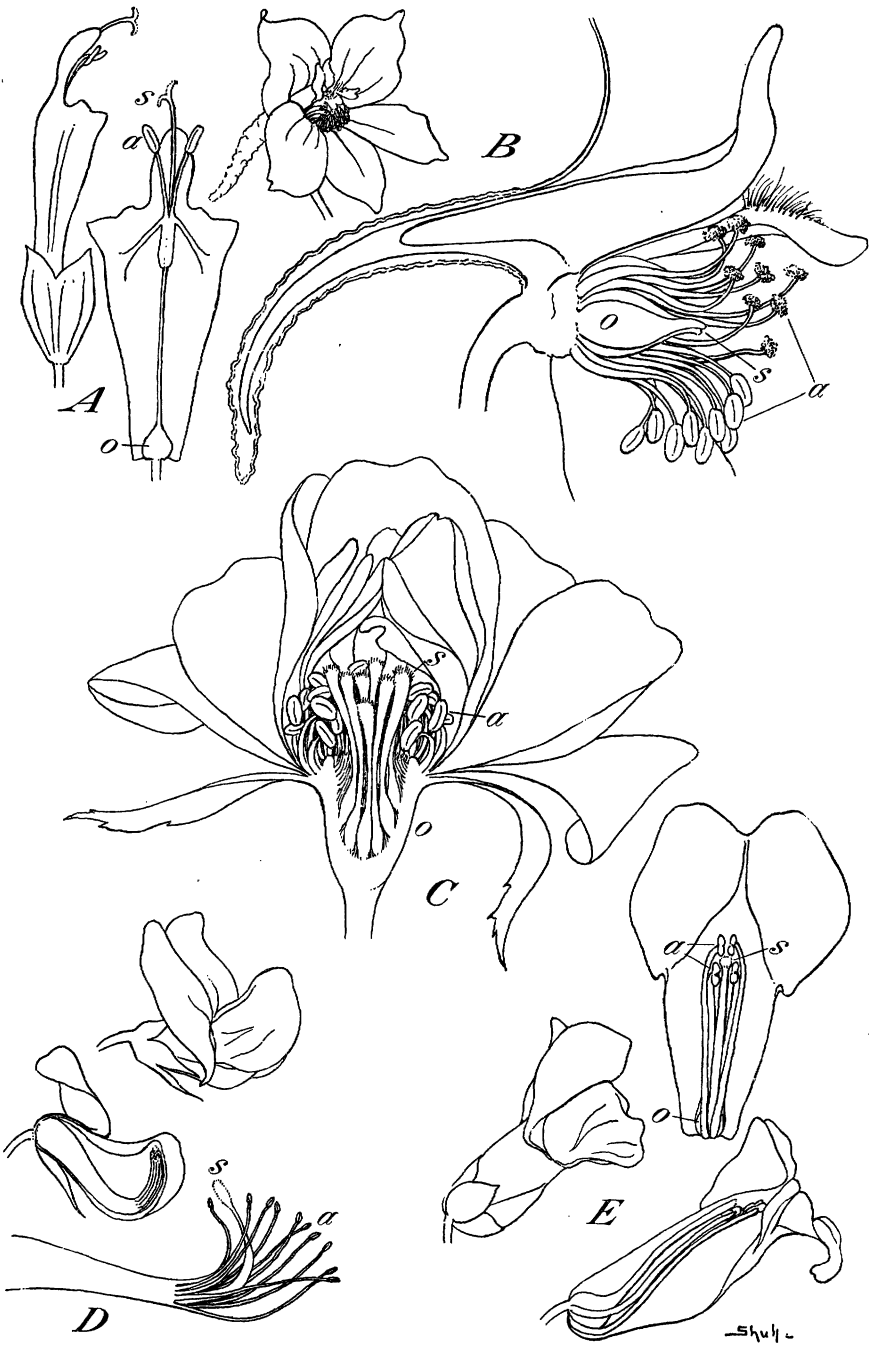
Figure 9.
(Legend on opposite page.)

In the nasturtium (fig. 8, *B*) the anthers form a tight cluster about the pistil. They are large and may be easily removed before they shed any pollen.

The gladiolus (fig. 8, *D*) has large anthers and a branching, plumelike stigma. Emasculation is very easily accomplished.

Phlox and verbena (fig. 8, *E* and *G*) are very similar in structure, and emasculation is practically identical for both. As can be seen from the illustration, the anthers are fastened to the inside of the tube formed by the petals and may be removed with the corolla, to which they are attached. This should be done just before the small bud opens, shortly after color has appeared in the folded petals. A slight pull at this time brings off the corolla tube with the anthers and leaves the stigma, which may be pollinated when it is receptive.

The carnations or pinks (fig. 8, *F*) also have a wide range of flower types. Only the single form is mentioned here. As can be seen from the figure, removal of the anthers is comparatively simple.

The scabiosa (fig. 8, *H*) is very similar to a composite flower. Here the so-called flower is actually a head of many small florets. In the figure a normal floret and one split open are shown. The anthers protrude so far beyond the stigma that their removal is easily accomplished.

The scarlet sage (fig. 9, *A*) has a rather unusual arrangement of its anthers. As shown in the illustration, they are held out from the flower wall by a bracelike arrangement. The stigma protrudes beyond them.

The larkspur (fig. 9, *B*) has a large number of anthers, which fit very closely about the stigmas of the compound ovary. The anthers may be removed with little injury to the flower, but caution must be exercised to get them all.

Roses vary from the single to the double form. The one shown (fig. 9, *C*) is a double hybrid tea. In emasculating, it is always advisable to clip away as much of the petals as possible. This gives ready access to the anthers, which can then be easily removed.

The sweet pea and the perennial pea are identical as far as emasculation technique is concerned. The sweet pea flower is one of the most difficult to emasculate without causing injury. The anthers, as shown in the perennial pea (fig. 9, *D*) form a closed column around the greater part of the ovary. They then branch out and closely surround the stigma. The removal of this column of anthers frequently injures the ovary, which is tender and brittle. It takes considerable practice to become skillful in the operation.

The snapdragon (fig. 9, *E*) is very easy to emasculate. The anthers do not shed pollen until the flower is fairly large. They may be removed readily without injury to the flower.

In figure 10 several members of the composite family are shown. While all have certain structures in common, there are also some differences that probably warrant a few words of explanation. In this large family of plants, the so-called "flower" is actually a group of

Figure 9.—Structure of (*A*) scarlet sage, (*B*) larkspur, (*C*) rose, (*D*) perennial pea, and (*E*) snapdragon to show arrangement of the parts concerned in pollination. The anthers, stigmas, and ovary are labeled *a*, *s*, and *o*, and in all instances each flower has been split open and drawn to show the relative position of these three parts. The technique for pollination of each is discussed in the text.
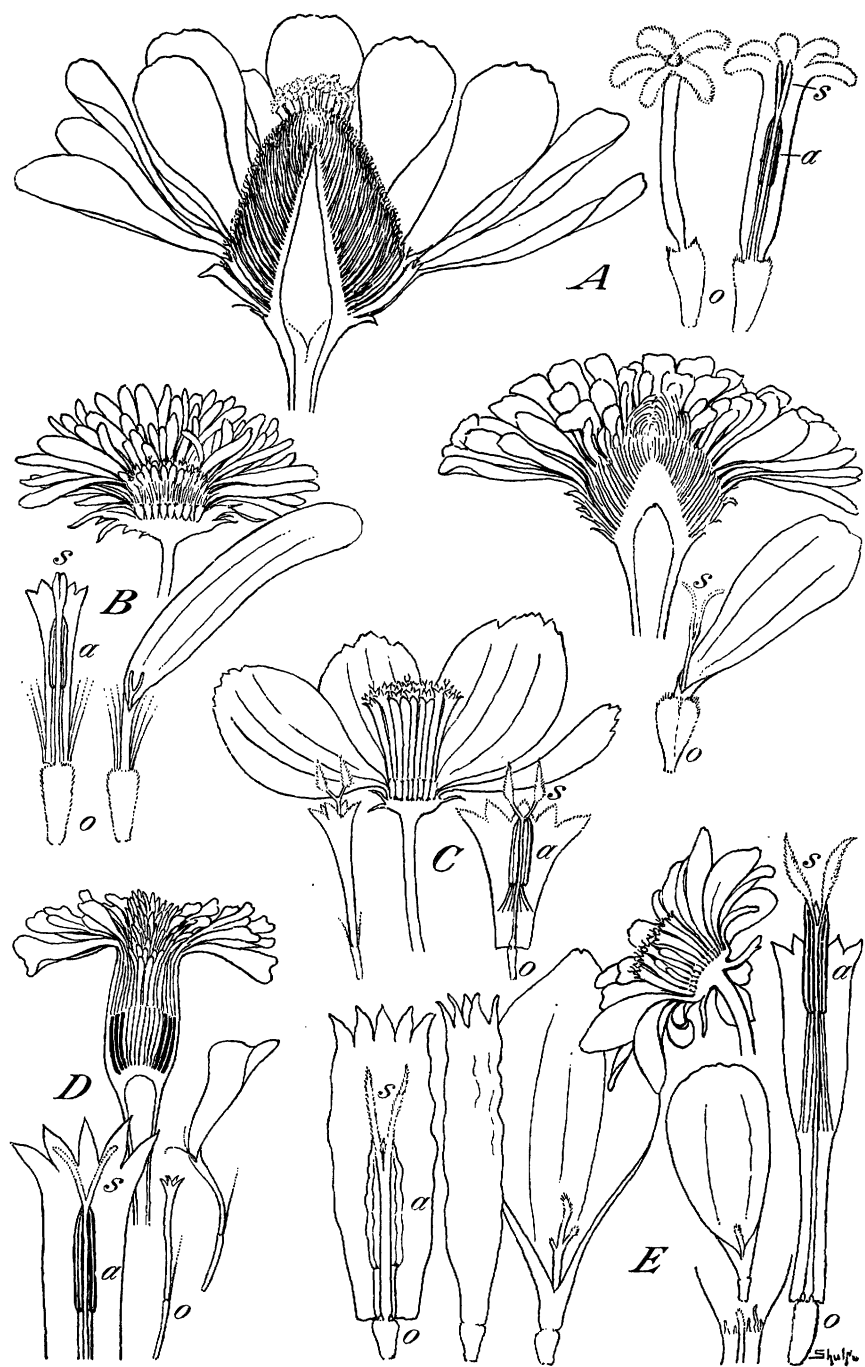
Figure 10.
(Legend on opposite page.)

many small flowers called florets, massed closely together in what is sometimes called a "head." These florets are of two distinct types. Some produce both pollen and ovules and are termed perfect flowers; others lack anthers for pollen production but have pistils for ovule production, and are called pistillate flowers. These small florets may also be classified as to the form of the corolla. In one type the corolla forms an inconspicuous tube surrounding anthers and style. These are found in the center of the head and are called disk florets. In the second type, called the ray floret, the corolla is modified into a conspicuous flat petallike structure, and extends far beyond other parts. The proportion between the two types varies considerably. The doubleness of any composite flower is determined by the number of ray florets. In extremely double flowers in this family, all the florets may be of the ray type.

The zinnia flower (fig. 10, *A*) occurs in at least four types. This information, as yet unpublished, was kindly furnished by C. F. Poole, of the Department. He is continuing his work on zinnias, which he started while a member of the staff of the College of Agriculture of the University of California.

The primitive or wild type is common in practically all races of zinnias. It is called "medicine hat" by seedsmen, and is illustrated at the top left of figure 10. The flower head has a single outer row of ray flowers, all of which are pistillate. The disk flowers are arranged in a somewhat pyramidal form and are all perfect. To the right of the medicine-hat type are shown a single perfect flower and one in which the corolla tube, which is the petal of the floret, has been split to show the anthers and style. Directly below this is shown a flower head of a second type, extremely double. Here all the florets are pistillate (female) and no pollen is found in the entire head. A single floret is shown below it in which the absence of anthers is conspicuous. Between these extremes are two intermediate types. One, more like the medicine hat, has several rows of pistillate florets and fewer perfect flowers. The second has a further reduction of perfect florets and more closely resembles the very double, purely pistillate flower head. Flower growers are interested chiefly in the more double types. These can set seed only if pollinated by some other type. A plant bearing only pistillate florets will certainly not set seed if it is grown under a cage or otherwise isolated from sources of pollen. This is probably the real explanation for some of the self-sterility in zinnias reported by some seedsmen when single plants were grown under cages. Sometimes more than one type of flower head is found on a plant. This condition has not been investigated.

From the above description it will be seen that cross-pollination in zinnias may be done without resorting to emasculation. If sterility factors are not present it is only necessary to make sure of the source of the pollen that reaches the stigmas of pistillate florets. In some

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Figure 10.—Structure of (*A*) zinnia, (*B*) aster, (*C*) cosmos, (*D*) marigold, and (*E*) dahlia to show arrangement of the parts concerned in pollination. The anthers, stigma, and ovary are labeled *a*, *s*, and *o*, and in all instances each flower has been split open and drawn to show the relative position of these three parts. The technique for .pollination of each is discussed in the text.

cases this may require the cutting away of perfect disk flowers, but in the purely pistillate double flowers no anthers are present and so no preliminary work is necessary.

As far as could be determined there is no report of any cross-breeding in the China-aster. It is likely that cross-pollinations have been made by amateurs and seedsmen, but no record of this has been available. A careful study of aster flower types (fig. 10, *B*) similar to that of the zinnia has apparently not been made. The aster flower head shown in the figure has both pistillate ray florets and perfect disk florets, and their proportion is a measure of the doubleness of the flower. If there is no complication from sterility, it should be fairly simple to control pollination. Small, curved, sharp scissors could be used to cut out all the perfect florets, and the remaining pistillate ones could then be pollinated as desired.

There is also a wide range of flower types in cosmos. The one illustrated (fig. 10, *C*) is a "single" type. All the florets are perfect, so that cross-pollination would here entail emasculation or removal of the anthers. Cross-pollination might also be done after using a stream of water to wash off all pollen after the two-parted, feathery stigmas have pushed their way through the anthers. If removal of the anthers is necessary, an excellent tool can be made by hammering flat the head of a pin, which is then bent and inserted in the end of a small wooden handle. By careful manipulation the corolla tube with anthers attached can be cut away. Unless considerable skill is attained, this operation will have a high mortality rate among the flowers on which it is used.

The marigold flower shown in figure 10, *D*, is very similar to the aster. There is, however, a wide range of flower types in marigold, as in nearly all other composites. In this flower there are several outer rows of pistillate florets, and those in the center disk are all perfect. The two types of florets are shown below the flower head with a perfect floret split open at the lower left to show anthers and stigma. Cross-pollination in this flower is essentially the same as in the aster.

In the dahlia (fig. 10, *E*) there is a range of flower types from the ordinary single to the complete double. In the single type the flower head is practically the same as the medicine-hat zinnia. In the outer row the florets are pistillate; the disk flowers are perfect. From this all gradations exist up to the fully double type, in which practically all the florets are pistillate. Since these pistillate florets do not produce pollen, few seeds are produced by the large double-flowered dahlias.

The flower shown here is an intermediate double type. To the left is a perfect disk flower as it looks when removed and split open to show style, stigma, and anthers. Self-sterility is the rule in garden dahlias. This makes crossing very simple, since emasculation is not necessary.

There are several precautions to follow in emasculating all flowers. The forceps or other tool used should be kept absolutely clean so that no pollen is carried from plant to plant. This can be done by holding it in alcohol for a minute or so before moving to the next flower. It is also necessary to keep the emasculated flower protected from any chance pollen. This is readily done by covering it with a bag until after the controlled cross-pollination has been made and fertilization has taken place.

The time to apply pollen is also sometimes a problem. In general, it should be done just as soon as the sticky fluid that develops on the

stigma makes it appear moist and shiny. This fluid holds the pollen grains and is nutritive material favorable to their germination.

Methods of Producing Superior Types of Flowers

The earliest and most commonly used method for breeding flowers is known as mass selection. It consists simply in saving for seed only the best plants of a variety. The procedure does not take into account the fact that better plants may be the result of either a better environment or a superior germ plasm. Since the seed from all the selected plants are mixed together before planting, it is difficult to evaluate any progress made. The method also does not differentiate between plants that are highly cross-pollinated and those normally self-pollinated; it is concerned only with the seed-bearing (maternal) parent. Most of our present flower varieties probably were developed in this way.

Mass Selection and Line Breeding

Mass selection does result in a gradual improvement even if some of the selected plants transmit poor germ plasm to the next generation, since the good ones have a better chance to be selected and in time predominate, gradually building up the variety. In this way desirable results are often secured, but frequently many years are required before the effects are noticeable. It is not true, however, even though commonly believed, that the selection process in itself is responsible for the gradual changing or improvement of a flower. There is little reason, in the light of our present information on plant breeding, to continue using this method. But even today it is the general practice among many flower breeders.

Following mass selection came so-called line-breeding. Here the breeder selected single plants and grew the seedlings from each selection separately. In this way the descendants of an individual plant could be studied, and the method was soon recognized as a considerable improvement over the earlier practice. It was possible to determine more readily whether an observed variation was hereditary (in the germ plasm) or simply an environmental modification. It also disclosed the status of a given characteristic in the heredity of a plant. If all the seedlings possessed the characteristic, it might be assumed that the plant was "pure" or homozygous for that characteristic and that it would be passed on to all the descendants; if some seedlings had it and some did not, the plant was heterozygous or mixed in its inheritance.

Unfortunately much of the single-plant-selection work of both amateur and professional flower breeders is done with open-pollinated plants—that is, no provision is made to protect from cross-pollination with other nearby plants. Of course, if a flower is normally self-pollinated, it may not be necessary to have this protection, but there are not many flowering plants that are entirely self-pollinated. The outstanding one supposed to be self-pollinated is the sweet pea. Here the stigma, completely surrounded by a group of anthers, is enclosed in that portion of the flower called the keel (fig. 9, *D*). When the flower matures the pollen is shed and falls on the stigma, which normally does not protrude from the petals forming the keel. In this manner the flower is supposedly protected from all pollen except its own.

Yet conditions in sweet-pea seed fields make this doubtful. If the sweet pea is entirely self-pollinated, it should be a simple matter to keep varieties pure (homozygous), since they could only acquire new genes by way of mutations. While the mutation rate in sweet peas has not been studied, the very large number of offtype plants (rogues) in sweet-pea seed fields certainly cannot be explained on this basis. In some instances these rogues are simply the result of accidental seed mixing, but this is not likely to occur in the case of the more careful growers, who keep their stock seeds separate. Very frequently, also, sweet-pea breeders encounter considerable difficulty in making a strain pure. An examination of several such cases showed that many of the flowers were not fully protected from cross-pollination, as had been assumed. The keel was not fully developed and was too short for the pistil and anthers. As a result the stigma very frequently protruded, even beyond the anthers, so that cross-pollination could easily have occurred.

There are some flowers in which the single-plant-selection method, depending on self-pollination, cannot be used. This may be due to self-sterility, as in some lily species, especially most forms of *Lilium longiflorum* Thunb., and in some iris, petunia, and *Nicotiana* species. Sometimes reasons other than self-sterility are responsible for failure of flowers to set seed when single plants are isolated. The pollen may be discharged before the stigma is receptive, or the reverse condition may occur. The structure of the flower may be such that self-pollination is impossible without the aid of some agency such as insects. Sometimes, as in species of *Lychnis*, the plants are either male (staminate) or female (pistillate). Such types obviously cannot be self-pollinated.

Single-plant selection or line breeding has many advantages over mass selections. When accompanied with self-pollination it quickly gives strains very uniform for habit of growth and other characters. All undesirable qualities are disclosed rapidly and may be eliminated within a comparatively few generations. Unfortunately, continued self-pollination frequently results in a loss of vigor. As a rule this weakened condition may be corrected by making cross-pollinations between inbred strains. This situation has received considerable attention from corn breeders and is discussed at some length in the 1936 Yearbook of Agriculture.

HYBRIDIZATION

A third method of flower breeding is the making of crosses between plants to secure new individuals that combine desirable qualities from each parent. While it is true that many of the early workers did cross-pollinate flowers, few realized the necessity of carrying their work beyond the first hybrid generation, called the F_1. In other words, if none of the hybrids was desirable, all were discarded.

The rediscovery of Mendel's work in 1900 demonstrated at once the importance of continuing into subsequent generations. Mendel showed that when two plants are crossed, each contributes to the heredity of the resulting hybrid. While ordinarily these contributions are exactly equal in quantity, they may vary qualitatively. When the two bits of heredity-carrying protoplasm, male and female,

are united in one individual, the hybrid, new combinations of characters become possible in the descendants of this hybrid. These new combinations may not be seen in the hybrid, but they will appear in some plants of the population descending from it.

Unfortunately, Mendel's basic laws are still unknown to many flower breeders. Each year many thousands of hybrid seedlings are undoubtedly grown and discarded as being inferior. If many of these had been carried into the next generation, it is likely that some worthwhile plants would have appeared. It is this second generation, commonly called the F_2, in which recombinations of parental characters are found.

In some instances the hybrid between two flowers is self-sterile. This commonly occurs when the two parents are from different species. Although the hybrid sets no seed with its own pollen, some seed may often be secured by crossing it with one or both of its parents. This is commonly called backcrossing. A backcross may be made in both directions; that is, the hybrid may be crossed to the maternal or the paternal parent. Sometimes a backcross will produce fertile seed in only one way, and as a rule it is more often successful when the hybrid is used as the maternal parent.

The method of improvement by hybridization will undoubtedly play an increasing role in flower breeding. It is the only way by which new combinations of desirable germ plasm can be effected. Very frequently a variety may be desirable in many ways, yet have some one characteristic that causes it to be unpopular. In many cases this character can be replaced by a desirable one from some other variety. A cross between them will provide an opportunity to combine the desirable traits of both parents in the F_2 or later generations. Some of the characters of one parent may be recessives, in which case they will not be apparent in the hybrid, but they will appear in some members of the next generation. Here, too, will be found the recombinations, that is, the new plants produced by combinations of characters from each parent. But since the genes, or carriers of heredity, are in the chromosomes, and all the genes in the same chromosome tend to be inherited together (this is the phenomenon known as linkage), we may find undesirable qualities associated with the ones we want. When this occurs it is necessary to grow populations large enough to get a reassortment of the genes or characters, which is brought about by what is called crossing-over, or the occasional exchange of material between chromosomes when the pollen grains and egg cells are being formed.

The backcross procedure mentioned above is probably one of the most valuable methods the flower breeder can use, and it should be more widely employed by amateurs and professionals. When two plants are crossed, usually the breeder has in mind some ideal type that he hopes to fashion by combining many desirable characters from one parent with fewer characters of the other. When this is true, it is best as a rule to backcross the hybrid to the more desirable parent. The resulting offspring may be again backcrossed one or more times and then self-pollinated. In a few generations the chances are that the desired inheritance of the best parent will be piled up and by selection the desirable characters of the other parent can be

retained so that plants closely approximating the ideal will be secured. The chief merit of this method is in recovering the quantitative characters of one parent from comparatively small populations in a relatively short time.

MUTATIONS

. In addition to the breeding methods already discussed, many varieties of flowers originate as mutations or sports. Mutations may arise in the pollen grains or in the egg cells, or they may occur in cells of the stems, leaves, flowers, or other portions of the plant. Many of our varieties of roses, carnations, and chrysanthemums have appeared in this way. Sometimes a side branch bears a flower differing in color or size from the remainder of the parent plant. When the plant can be propagated vegetatively, it is usually a simple matter to introduce the changed form or mutant as a new variety. For some as yet unknown reason, certain varieties of some flowers are especially noted for the number of bud sports they have produced. This is particularly true of the Ophelia rose. Many of the present-day varieties of greenhouse carnations are also mutations of this sort.

When a mutation occurs in a sex cell it does not appear until the next generation. If it is a recessive and the parent plant normally is cross-pollinated it may not show up for several generations. It is entirely probable that some of the new characters that appear in a variety of flowers grown from seed arise as sex-cell mutations. The vast majority of the so-called "breaks", however, are not mutations but simply recombinations of already existing characters following cross-fertilization (fig. 11).

Since the chromosomes are the carriers of the hereditary units, any changes in them should have an effect on the plant. Such a change may effect a rearrangement of the genes in a single chromosome or even the loss of some of them. Sometimes a whole chromosome is lost or an extra one added, or each chromosome is reduplicated so that the entire number is doubled. Occasionally one may be broken and the fragment retained or lost. The plant that results from any of these changes is likely to be different from one with normal chromosomes.

The doubling of the chromosome number may occur in several ways. The sex cells sometimes form with all the chromosomes present rather than half the number, which is normal for sex cells. In other instances an ordinary cell in a stem or root may double up its chromosome number, and then when this doubled cell divides all its descendants will have the doubled number.

A well-known example of the doubling of the chromosome number in stem cells is the case of *Primula kewensis* W. Wats. (Kew primrose), as reported by Digby (*111*) in 1912, and by Newton and Pellew (*390*) in 1929 (fig. 12). It is a desirable primula, now quite commonly grown by many florists. It originated in this manner: A cross was made between the species *P. floribunda* Wall. (buttercup primrose) and *P. verticillata* Forsk. (Arabian primrose). The hybrid was completely sterile for many years, when there suddenly appeared on one plant a branch that bore large fertile flowers. The chromosome number of both *floribunda* and *verticillata* is 18, and that of the large-flowered branch was 36. Undoubtedly this branch arose from a cell that had doubled its chromosome number.

Another interesting instance of the origin of a large-flowered plant as a result of chromosome doubling was reported in *Campanula persicifolia* L. (peachleaf bellflower) by Gairdner in 1926. The normal species has 16 chromosomes, and from it came a seedling with 32 chromosomes. The doubling of the chromosome number resulted in a considerable increase in size, and the new variety was named Telham Beauty.

Quite recently, Randolph (*423*), of the Bureau of Plant Industry, in cooperation with Cornell University, has developed a method by which chromosome numbers of corn may be doubled. While no report has as yet appeared concerning its use for doubling chromosome numbers of flowers, it seems likely to play an important role in future flower breeding. The results are secured by the application of heat to the flower just after fertilization has taken place. The time between application of pollen to a stigma and the actual union of the two sex cells is very variable. It may require only a few hours or it may take several days. The new cell formed by the union of the two is the first cell of the young embryo. This one-celled embryo usually does not divide for some time, and it is during this
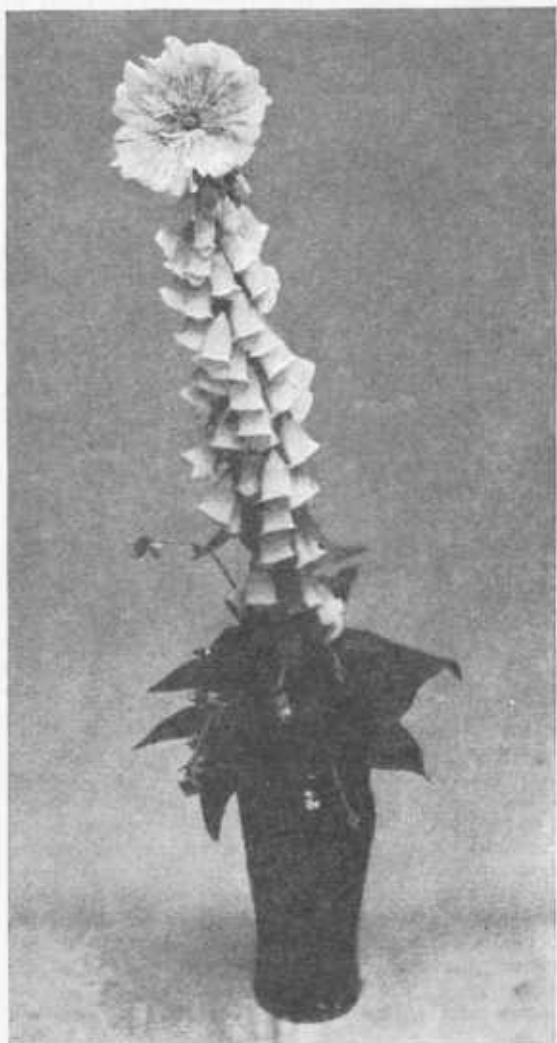
Figure 11.—A horticultural form of foxglove in which the top flowers are united to form a round, hollyhocklike flower. This photograph was sent to the senior author as representing a possible new mutation supposedly arising spontaneously in a home flower garden. It is a form that is not widely distributed but has been known for a long time. It is recessive, so that when crossed with "normal" all the hybrids are normal and the next generation is composed of 3 normal to 1 abnormal.

period just at or before division that heat is applied. Since the temperature necessary is very likely to be different with different plants, it can be seen that a considerable amount of preliminary investigation will be needed before this method can be used with certainty.

There are on record several cases of spontaneous doubling of the chromosomes in the one-celled embryo. The one of interest here, because the parents, commonly called flowering tobaccos, are frequently found in flower gardens, is that of *Nicotiana digluta* Clausen and Goodspeed. Clausen and Goodspeed (*76*) reported a plant with 72 chromosomes coming from a cross between *N. glutinosa* L. with 24 chromosomes and *N. tabacum* var. *purpurea* with 48 chromosomes. All the hybrids should have had 36 chromosomes, but this one plant had 72. They believed that this particular F_1 plant had doubled its chromosome number shortly after fertilization. There is also evidence of a similar occurrence in tomatoes. In general the doubling of the chromosome number is usually accompanied by an increase in the size of the plant and flower.

Chromosomes may also be modified in structure. The modification may result from the breaking of a chromosome into

Figure 12.—Diagrammatic drawing showing the effect of the doubling of the chromosome number in a species hybrid. The plant is a cross between (*a*) the Arabian primrose (*Primula verticillata*) and (*b*) the buttercup primrose (*P. floribunda*). It has 18 chromosomes, like each of its parents (the chromosomes are represented near one of the upper flowers). Suddenly it produced the lower branch with larger flowers, and this was found to have 36 chromosomes (represented on one of the petals). Whereas the hybrid itself was sterile and set no seed, the new branch with 36 chromosomes was fertile and set seed. This fertile side branch was the progenitor (*c*) of the well-known Kew primrose (*P. kewensis*).

several parts, or from a slight change in one of the genes that it carries. There are many recorded instances of such changes occurring in nature. Frequently they cause freakish and abnormal plants, but they are also responsible for many worth-while new variations. Until recently these changes were purely chance occurrences over which the breeder had no control. Recently, however, certain external agents such as X-rays, radium, ultraviolet light, heat, and some chemicals have been shown to be effective in producing them.

Artificial Methods of Changing Germ Plasm

The use of X-rays, radium, and ultraviolet light for the production of new flower types will probably not become general. Considerable danger is involved, and the work should be done only by thoroughly trained technicians. The actual manner in which these agencies cause the chromosome to change is not known, but the very short rays seem to incite rearrangement of genes and even chromosome breaking.

Some of the earlier work showing the effect of X-rays and radium on flowers was done by T. H. Goodspeed (fig. 13) and his associates at the University of California. The plants were several species of ornamental tobaccos. Both seeds and sex cells were exposed to the action of radium and X-rays. In the case of ungerminated seeds there followed a very noticeable retarding of germination, but at maturity no general effect of X-radiation of the seeds could be seen. If, however, the seed was germinating or if tiny seedlings were X-rayed, many changes in growth and form were noticed.

In another series of experiments by Goodspeed and Avery (145), sex cells were exposed to X-rays. This was done by X-raying buds

Figure 13.—T. H. Goodspeed, professor of botany, and director, Botanical Garden, University of California, Berkeley. One of the pioneers in the use of X-rays and radium to induce mutation in plants.

in which the egg mother cells were just beginning to go through the series of divisions that give rise to the egg cells or female gametes. After this treatment these buds were pollinated with pollen from untreated flowers. Now if a change occurred in an egg cell and this egg cell was pollinated by normal pollen, the new condition would show up at once if it was a dominant. If the new character was recessive, however, it would not appear until the next generation.

Following this treatment many plants were secured that differed markedly from their sister untreated plants. One of these variant plants was selected for further study and was self-pollinated. After six generations, that is, six cycles "from seed to seed", seven pure-breeding new types and seven not yet fixed have been secured. Some of these new types differ so markedly from their un-X-rayed sister plant that they probably are entirely new varieties, and even in a few instances new species. They differ from one another and from the untreated plant in habit of growth, in form of leaf, flower, and capsule, and even in the color of leaf and flower.

This series of experiments is remarkable in several respects. It is the first to demonstrate the possibility of actually securing fertile new

types of flowers by X-raying sex cells. All 14 types came from a single X-rayed egg cell, which was pollinated by an untreated pollen grain.

Recently there has appeared another report of effects of X-raying a flowering plant. In the laboratory of the General Electric Co. at Schenectady, N. Y., Moore (*374*) exposed Regal lily bulbs to X-rays. Among those so treated, two upon blooming showed an unusual behavior of the anthers. The flowers differed only slightly from the normal Regal, but the anthers did not open and shed their pollen. Since the pollen is considered unsightly when scattered on the petals, this nonshedding habit is considered by the originator as valuable. These plants are easily propagated by divisions of the old bulb so that they can be multiplied without recourse to seed and also with the certainty they will all be identical, unless there is a reversion to the normal.

Another series of interesting experiments with X-rays was conducted by Morgan (*377*), who exposed seeds, flower buds, and corms of freesias to various dosages. Very little effect was noticed on seed and flowers except when exposures were strong and for rather long periods. The corms, however, showed decided effects from the rays. The untreated corms produced single plants, while as many as five "shoots" were produced by a single X-rayed one. The treated corms also started to germinate immediately after planting, made more rapid progress, and showed curling and twisting of leaves and stems; and the flowers were split and deformed. In general, the effect of X-ray treatment in low dosage seemed to be an acceleration in the rate of growth and the stimulation into growth of structures that otherwise would have remained latent. With increase in intensity of the dosage, the acceleration was lost and the rate of growth was even retarded. The heaviest dosages killed the corms.

In another similar series of experiments, tulip bulbs were exposed to X-rays by Van Heijningen and his associates (*197*) at the Wageningen station in the Netherlands. In many instances the results parallel those with the freesia corms. After moderately strong exposures, the number of small increase tulip bulbs was slightly more than in untreated bulbs. The flowers produced by the treated bulbs in some cases had irregular incisions on the petals, quite similar to those in the so-called Parrot varieties.

Not much in the way of practical results has been accomplished as yet by using artificial physical methods to induce changes in the germ plasm. This is not surprising, however, when it is remembered that although earlier sporadic attempts had been made, less than 10 years have passed since the present type of research was started. Much of the recent and current work of this type with flowers and other plants is still in the experimental stage. Enough has been done to indicate that plants, and even parts of the same plant, differ in response to the same dosages of rays. This means that much preliminary work is necessary merely to discover what dosages to use. There has also been too great a tendency for some to rush into the work while lacking a proper background in genetics and plant breeding. Instances are known in which seeds or pollen have been X-rayed, and when nothing unusual appeared in the resulting plants the entire

lot was discarded. If any recessive changes in the germ plasm were effected, they might not appear until later generations. In this connection it is recalled that Goodspeed continued his work into many succeeding generations and located numerous definite new types. In much of the work also, the number of treated individuals is very small. If the frequency rate of valuable changes is but 2 or 3 in 1,000, there will be little chance of securing them when only 10 to 20 seeds or plants are treated.

WHAT THE STUDY OF CELLS CONTRIBUTES TO FLOWER BREEDING

THE trained breeder likes to know the number of chromosomes in the plant with which he is working. For one thing, it determines the number of individual plants he will have to grow to get a desired recombination of the characters in which he is interested. Suppose, to take a purely imaginary case, that a certain plant has oblong red petals. The breeder wants to get a hybrid with the red color, but does not want the oblong shape. Now if this plant has four chromosomes in its sex cells, the chances are one in four that these two characters are linked—that is, they are in the same chromosome and will usually be passed on together in inheritance. But if there are eight chromosomes, the chances are only one in eight that they will be linked. In the latter case, he has twice as great a chance of getting one character without the other. The smaller the number of chromosomes, the greater the chance of linkage among any two or more characters and the larger the number of individuals that will have to be raised in an attempt to break up the linkage by crossing-over.

Another point of interest to the breeder is the important part that chromosome numbers appear to play in the probability of securing fertile crosses between two species. When both have the same number, the chances for success are much greater than when they differ. There are, however, many instances of hybrids between species with different numbers of chromosomes. As a rule such crosses are more likely to be successful when the one with the greater number of chromosomes is used as the maternal parent. There are, however, a few instances where crosses have been successful even when the species with fewer chromosomes was the maternal parent.

In addition to the question of linkage, the chromosome number may throw light on other questions. For instance, the lilies commonly have 12 chromosomes in their sex cells, which means that they have twice 12 or 24 in their body cells (12 pairs). Now for years the so-called Tiger lily (*Lilium tigrinum* Ker) was noted for its persistent self-sterility. Recently it has been shown to have 36 chromosomes in its body cells instead of 24—3 of each kind instead of 2 of each kind.[4] This is an abnormal condition, but it occurs fairly commonly in plants, and it often accompanies or causes sterility. There are also plants with four times the basic or sex-cell number of chromosomes, or five times, or six times, and even some plants that retain the basic or single number in the body cells instead of doubling this number, which is the normal method. In some species of plants, different

[4] A fertile *tigrinum* has been reported rather recently. According to Stout it varies somewhat from the older common form and apparently has 24 chromosomes rather than 36. It is therefore a diploid.
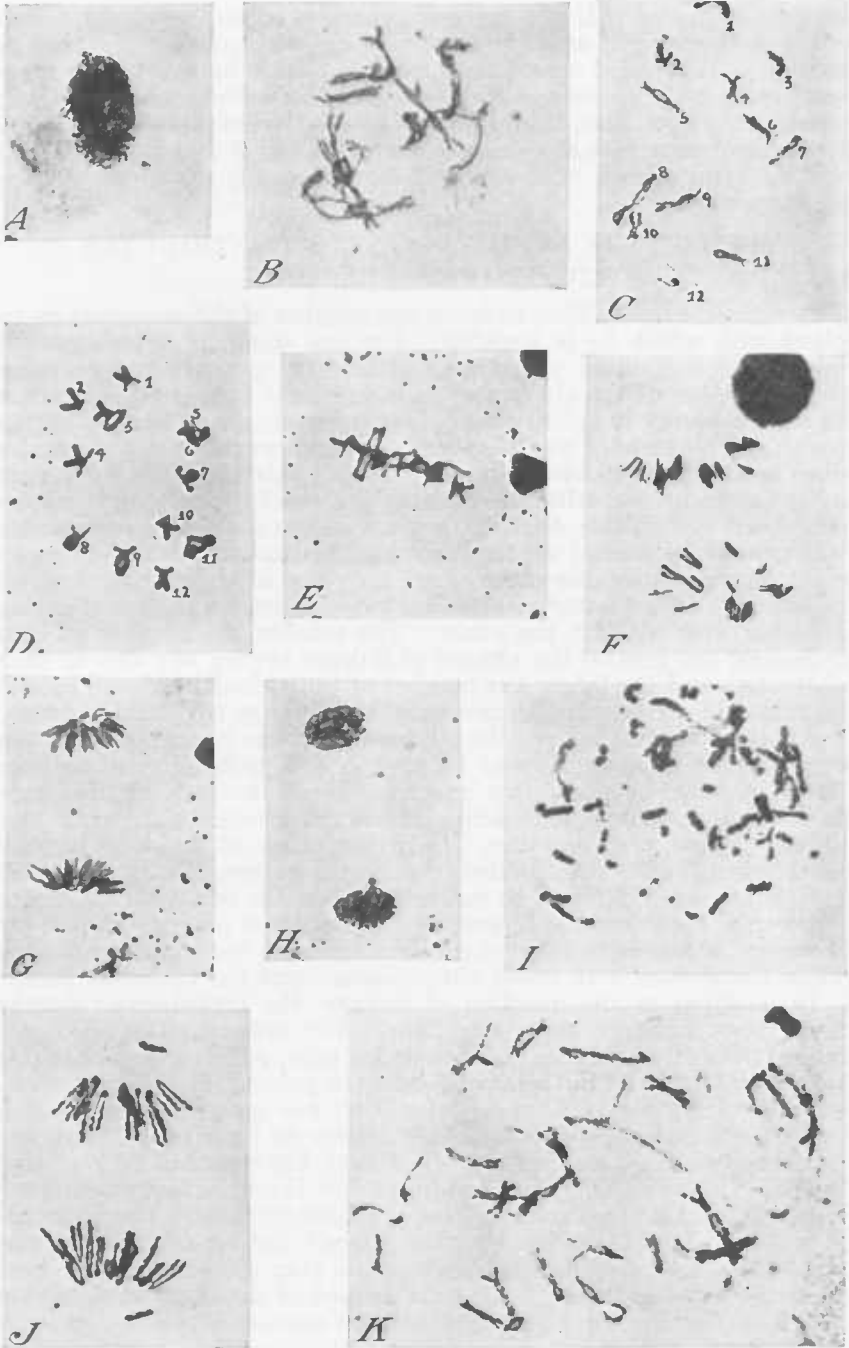
Figure 14 (legend on opposite page)

varieties run a whole series of these numbers. Thus in the lilies there might be one variety with 12 chromosomes in the body cells (haploids); another with 24 chromosomes (diploids) as shown in figure 14; another with 36 (triploids); another with 48 (tetraploids); another with 60 (pentaploids); another with 72 (hexaploids). Hereafter, these names will be used to indicate the number of times the basic number is multiplied in the body cells of the plant.

VARIATIONS IN CHROMOSOME NUMBERS

The question now arises as to how the knowledge that the Tiger lily is a triploid can possibly aid flower breeding. To answer that, it is necessary to give some preliminary discussion. First, it will be remembered that normally the sex cells of a plant always contain half the number of chromosomes in the body cells. This reduction in the number of chromosomes is one of the things that happens when a cell gets ready for reproduction. Now there are many known triploids in plants, and without exception they are all highly self-sterile, but some will set seed when pollinated by a diploid. It is probable that these triploids arise in two ways.

(1) A tetraploid type may be pollinated by a diploid. For instance, in the China-aster the basic or haploid chromosome number is 9, so that a diploid would have 18 chromosomes and a tetraploid 36 in its body cells. When the reproductive cells are formed, these numbers are cut in half; the sex cell of the diploid has 9 chromosomes and that of the tetraploid 18. Now the two sex cells join. Nine chromosomes are added to 18 chromosomes, and the result is 27 chromosomes, or a triploid, since 27 is three times the basic number.

(2) The male or the female nucleus of a normal diploid cell may fail to reduce its chromosome number in preparing for reproduction. In this instance it would keep 18 chromosomes instead of reducing the number to 9. When it united with a normal sex cell having 9 chromosomes the total would be 18 plus 9, or 27 — a triploid.

Figure 14.—Chromosomes and formation of pollen grains in the Easter lily as seen under the microscope ($\times$ 350). *A*, The cell that will divide twice to form four pollen grains. The chromosomes are all long fine threads and form a tangled knot. *B*, After the first division is well started; the knot has unraveled and the chromosomes are pairing. Since the lily has 24 chromosomes, there should be 12 pairs. *C*, The division has progressed to where 12 pairs of chromosomes can be seen very clearly. *D*, A little later stage of division, in which the chromosomes have become shorter and thicker. The 12 pairs are all clear with the exception of no. 5, which lies under no. 6. *E*, A side view of the 12 pairs just as they are about to separate. *F*, Here 12 chromosomes have moved to each of two sides of the cell and the first division is almost completed. *G*, The 12 chromosomes in each group are now organizing new cells and getting ready to divide again. *H*, There are now 12 chromosomes in each dark-stained nucleus, and each nucleus will again divide to form 4, which finally become pollen grains, each with 12 chromosomes. *I*, Occasionally in the Easter lily something happens that causes the chromosomes to break into many small pieces. Such results can be accomplished by use of X-rays, radium, and possibly heat treatment just before the cells start to divide. *J*, In this cell 11 of the 12 chromosome pairs behaved normally, but two chromosomes probably did not pair. They are the ones at top and bottom. *K*, A giant (tetraploid) cell with 48 chromosomes instead of 24. Such cells are not known to have given rise to any tetraploid lily plant.

Tetraploid lilies are not known to occur, and it is therefore assumed that the triploid form must have arisen in the latter fashion—though there may have been a tetraploid parent that has not been discovered or that has become extinct.

If a triploid is not valuable in itself, there is usually little reason for using it in a breeding program. As a rule, when it is crossed with a diploid, the resulting hybrids are inferior, usually being dwarf, self-sterile forms. If their chromosomes are examined they are found to vary in number from plant to plant. Thus a few successful crosses between the Tiger lily and other lily species have so far given only small deformed seedlings. It has already been noted that the Tiger lily has 36 chromosomes, the other species 24. While no evidence is available as to the chromosome numbers in the hybrids, it is very probable that some had 24, some 25, 26, 27, etc.

As more and more is accomplished in chromosome studies of flowers, it is likely that we shall find other instances similar to the Tiger lily. If a valuable triploid flowering plant appears and can be propagated by cuttings, it is not essential that it be fertile and bear seed. For instance, a valuable triploid carnation, chrysanthemum, rose, narcissus, or geranium could easily be increased by division. With suitable developments in technique it might be possible to create other triploid forms as fine as the Tiger lily.

OTHER CHROMOSOME PECULIARITIES

Sometimes a variety persists in producing year after year a number of peculiar variant forms. Even though it is carefully self-pollinated the variant forms may reappear with great regularity. Such a plant cannot be made to breed true, and sometimes the situation is the result of the structure and behavior of its chromosomes. Keeping in mind that the chromosomes carry the hereditary genes it is not strange that these peculiarities of inheritance can be traced to abnormalities in chromosomes.[5] Such plants may show a peculiar behavior of their chromosomes when sex cells are formed, as has been conclusively demonstrated by cytologists working with the evening-primrose.

One of these evening-primroses, known as Lamarck's, produces several variant forms year after year. At first plant breeders thought these were distinct changes in genes in the chromosomes. They were called mutants and the change in the gene was thought to have happened when the sex cells were formed or before. Careful cytological study of chromosomes in the sex cells demonstrated that the evening-primrose chromosomes act very irregularly while pollen grains and egg cells are being formed. These irregularities result in some few sex cells receiving an unusual combination of chromosomes. Since chromosomes are the carriers of hereditary characteristics, such peculiar sex cells naturally give rise to unusual and unexpected seedlings. Unless the sex cells had been examined under the microscope, we would have continued believing that the evening-primrose produced a very large number of mutations. This might have led us into other errors by encouraging the idea that mutations are relatively common. In fact this belief does exist among many amateur and

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[5] This statement has some exceptions, chiefly a few instances of cytoplasmic inheritance, dependent on the cell material outside the nucleus.

professional flower breeders. It is expressed in the claim of the sudden appearance of what are commonly called "breaks", which follow the crossing of two varieties. Thus we often see it stated in a popular article that some new flower originated as a break from the hybrid made by crossing two older varieties. It is unquestionable that mutations do occur now and then, but they are comparatively rare. The chances are preponderantly in favor of the breaks actually being recombinations of characters that already existed in the two parents.

A situation that appeared to be somewhat similar to the evening-primrose problem was called to the attention of the senior author of this paper several years ago in California. The late J. H. Franklin, of the Waller-Franklin Seed Co., told of a peculiar breeding behavior in annual larkspur. He had been working for years with a pink-flowered form called Exquisite Pink. The shade of color and the habit of the plant were very desirable, and it was popular with florists. Unfortunately he had not been able to get a pure-breeding strain. Year after year his best selections produced the same variant forms. These undesirable types included a white-flowered form, a rose, a blue, a rose with blue flecks on the petals, a white with blue flecks, and a purplish blue. He sent some seed to the California Agricultural Experiment Station at Davis, where it was grown, and the plants were studied. For 2 years, Exquisite Pink plants were self-pollinated and each time they produced the same variant types. The next year microscopic slides were made of the developing pollen grains, and some of the same general types of irregularities were found that occur in the evening-primrose. Apparently some structural peculiarities in the chromosomes were causing the difficulties. This meant that the Exquisite Pink larkspur could never breed true. When this was explained to Dr. Franklin, the strain was discarded. New selections were started with other pink-flowered forms, and at present there are several good pink larkspurs available.

One of the most popular flowers for both breeding and cytological research is the stock, *Matthiola incana* (L.) R. Br. This plant is unique in that it has two distinctive types, the single- and double-flowered forms, the latter containing no anthers or pistils and making no seed whatever. Reproduction, then, is from seed produced by the single flowered plants. The growers of stocks, both florists and amateurs, are interested almost exclusively in the double forms. For some time plant geneticists have known that there are three types of single plants. One when self-pollinated produces no doubles, the second produces about 25 percent of doubles, and the third from 54 to 56 percent. Obviously the third type is the one to use for seed. It is called ever-sporting because of the high percentage of doubles it produces.

The problem of explaining the peculiar behavior of the ever-sporting stock attracted many workers. One quite logical explanation assumes some condition that kills half the pollen grains and approximately 6 to 8 percent of the egg cells. This might be caused by what is called a lethal gene located in the same chromosome as the gene for singleness. The lethal gene would have to be recessive since if it was dominant all plants with this gene would die. Being recessive a plant can carry the gene and its normal allelomorph and be able to live. Let us use the symbol a for the lethal gene and the symbol A to represent the normal

allelomorphic gene that is dominant to *a*; then all plants of the *aa* type would die, but *Aa* plants would live.

Now singleness in these stocks is dominant to doubleness.   Single-flowered plants may be pure (homozygous) for singleness, or they may be hybrid (heterozygous) for this character.   A pure (homozygous) single gives only singles when it is self-pollinated.   A heterozygous plant gives 3 singles to 1 double.   According to the above theory, the third type, the ever-sporting race, should be hybrid (heterozygous) for singleness and for the linked lethal, which would result in 54 to 56 percent of doubles instead of only 25 percent.

In 1931 Philp and Huskins (*408*) published a cytological study on ever-sporting stocks that apparently explained the situation.[6]   In order to understand their work it is necessary to recall that only one of each pair of chromosomes occurs in a sex cell.   The pair of chromosomes of which one member carries the gene for doubleness and the other member the gene for singleness, therefore, never get into the same sex cell.[7]   Philp and Huskins are able to show that ever-sporting single plants had one pair of chromosomes that differed from one another in appearance, one lacking a small knob on its end.   This is very significant when it is remembered that the two chromosomes of a pair normally have an identical shape.   From their work, they stated that the pollen grains getting the chromosome lacking the knob did not function.   In other words, the absence of the small knob acted as a lethal to the pollen grains in which it occurred.

If only the "double" pollen grains can function, while both "double" and "single" eggs are good, it is easy to see how such plants produce about half doubles and half singles.   The fact that the ratio is not exactly 50–50 is explained by assuming that a few egg cells getting the chromosome lacking the knob do not function.   This explanation was verified to some extent by a study of pollen germinations from pure and ever-sporting singles, which showed that germination of ever-sporting pollen was only about half that of pollen from pure singles. Evidently about half the pollen grains of an ever-sporting single were being killed in some manner.

The entire situation is much clearer if figure 15 is studied.   At the top are shown the seven pairs of chromosomes of a single-flowered ever-sporting stock plant.   The members of each chromosome pair look exactly alike with the exception of the first.   One lacks the little knob on one end, which cytologists call a satellite.   A large *S* is printed before the one that lacks the satellite.   This is to represent the gene for singleness, which it carries.   Its mate (homologue) has a small *s* to represent the gene for doubleness, which is recessive.   The chromosomes of the eggs and pollen grains produced by this single-flowered plant are also shown.   They are of two types, I and II, and half the eggs are of one and half of the other type.   This is also true of the pollen grains.   According to Philp and Huskins, however, only those pollen grains with the satellited chromosome function, and all the eggs live except about 6 to 8 percent of those lacking a satellite. Since only one type of pollen grain lives, there will result just two types of plants.   They are shown at the lower part of the diagram.

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[6] This work has recently been questioned by Vestergaard and may need further investigation.
[7] This actually happens occasionally, as discussed earlier, when a diploid sex cell is formed.

One will be single, since it receives the knobless chromosome with the single gene, and the other will be double, receiving two double-flowering (*s*) genes and two satellited chromosomes. Since there are not quite so many eggs carrying the large *S* for single flowers, the result is about 54 to 56 percent of doubles and 44 to 46 percent of singles. Philp and Huskins report that all doubles examined by them had two
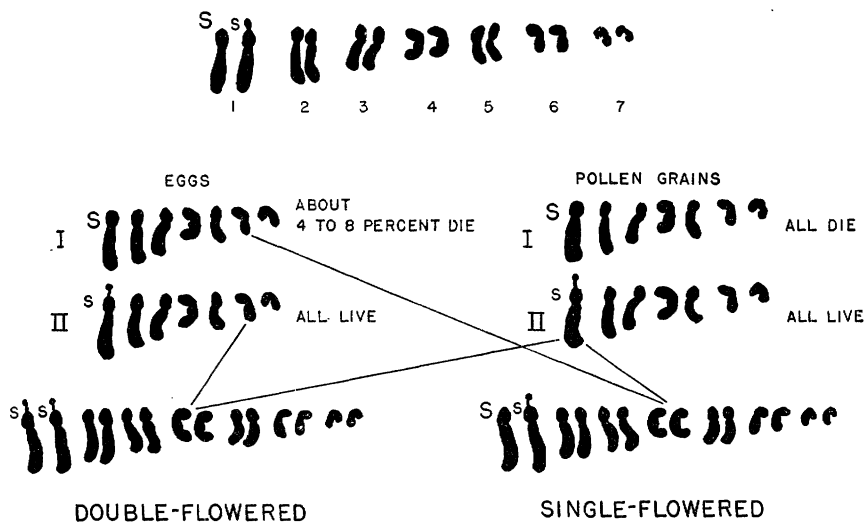

Figure 15.—The chromosome situation in ever-sporting, double-flowering stocks.

satellites, while all singles had but one. This refers, of course, only to the ever-sporting races.

Another cytologist, Frost (*135*), working with stocks, has also demonstrated the value of cytology to flower breeding. He has shown that the proportion of double-flowered plants may be increased very materially. Among the various types of stocks he had in his experimental plot was an ever-sporting form known as Snowflake. In this variety he found a peculiar single-flowered plant that had very narrow slender leaves. When this plant was self-pollinated it gave about 47 percent of singles and 53 percent of doubles. About 37 in every 100 plants had the narrow slender leaves of the parent. Also, these plants were very weak in growth and had no decorative value. The remaining normal plants descended from this narrow-leaved parent were found to be about 90 percent of doubles. Since the slender leaves are conspicuous even in the seedling stage, the plants having them may be discarded at that stage, and among the remaining plants there will be only about 10 percent of singles. In order to continue this situation, however, it is necessary that seed be saved only from the slender-leaved types.

The explanation for this interesting condition was worked out by making a cytological study of the chromosomes of the slender plants. In addition to the 14 chromosomes expected, these plants showed a small chromosome piece, which cytologists commonly call a fragment. These plants, then, had 14 + 1 chromosomes. Evidently this frag-

ment was the part that carried the gene for singleness or doubleness. Since only slender-type plants had this fragment, it was concluded that the slender leaves were also caused by its presence. Since a gene for singleness was also in the fragment, these two characters, singleness and slender leaf, behaved as linked genes do; that is, they tended to remain together from generation to generation. Thus if the slender plants are discarded in the seedling stage, it means the removal of most of the singles. This very unique scheme is not in practice as yet, probably because it is not understood by the average flower breeder.

Since the chromosome number of a plant does have considerable importance in breeding work, a list of chromosome numbers of some of the most common flowers is given in table 1.

TABLE 1.—*Chromosome numbers in some of the commoner flowers*

Name of flower	Chromosomes in—		Name of flower	Chromosomes in—	
	Sex cells	Body cells		Sex cells	Body cells
	Number	*Number*		*Number*	*Number*
Ageratum	10	20	*Dahlia variabilis*	32	64
Alyssum	8	16	English daisy	9	18
Annual larkspur	8	16	Fuchsia	11	22
Bachelor button (cornflower)	12	24	Lily, Easter	12	24
Calendula	14	28	Lily, tiger		36
California-poppy	6	12	Nasturtium	14	28
Canterbury-bells	8	16	Rhododendron species	13	26
Canterbury-bells (tetraploid)	16	32	Roses, various types	7, 14, 21	14, 28, 42
China-aster	9	18	Snapdragon	8	16
Chrysanthemum	9	18	Stocks	7	14
Clematis	8	16	Sweet peas	7	14
Columbine	7	14	Sweet-william	15	30
Cockscomb	18	36	Wallflower	7	14
Dahlia (some types)	16	32	Zinnia	12	24

SOME PAST ACHIEVEMENTS AND FUTURE POSSIBILITIES

THE fundamental principles of breeding are now fairly well established, but the methods of application vary with different plants. The plant breeder who is interested in flowers and ornamental plants is faced with the problem of choosing his material from among many hundreds of species. It is obviously impossible to work with more than a small proportion of them. As a rule those breeders who have accomplished the most have limited themselves to a very few.

In preparing this article, the authors also were confronted with the task of choosing only a few representative species out of many available. In doing this it was realized that much interesting and valuable work would necessarily be left out. To some extent this omission is compensated for by the extensive appendix on research in flower breeding at the end of this article. Those especially interested in some flower not mentioned may find it included there.

AMARYLLIS

Botanically the name amaryllis should refer to the entire family Amaryllidaceae, but horticulturally it is used for plants of a single genus, *Hippeastrum*, belonging to this family.

A watchmaker named Johnson, of Lancashire, England, is credited with having produced in 1799 the first hybrid amaryllis recorded in the history of this plant. Johnson had a small garden where he followed his hobby of hybridizing plants and produced *Hippeastrum johnsoni* Bury, which even by modern horticultural standards was a distinct and outstanding variety. This hybrid is recorded as a cross between *H. reginae* Herb. and *H. vittatum* Herb. It has since been used a great deal as a parent in the production of other hybrid amaryllis.

It was at the end of the eighteenth century that widespread interest began to be centered on plants of the amaryllis family. In 1821 William Herbert published a treatise on plants included in the amaryllis family. This was followed in 1837 by his work entitled "Amaryllidaceae", which is still considered a valuable record of the amaryllis family. In this book Herbert lists under the genus *Hippeastrum* 31 "hybrid or mixed crosses" which he had secured or which had been produced by others and brought to his attention.

The family of De Graaff, of Leiden, Netherlands, was also greatly interested in the amaryllis at the beginning of the nineteenth century and produced hybrids that were of importance at that time. Following closely was the famous English firm of James Veitch & Sons, which introduced two handsome species from the Andes of Peru, *Hippeastrum pardinum* Dombr. and *H. leopoldi* Dombr., which were first flowered at Chelsea, England, in 1867 and 1869, respectively. From these two species have come many beautiful hybrids. A list of those who have made noteworthy contributions to the development of the amaryllis in the last 50 years includes such names as Arthington Worsley in England, E. H. Krelage in the Netherlands, E. L. Holmberg of Argentina, and Henry Nehrling and Theodore L. Mead of the United States.

As is the case with many horticultural plants, botanists find it difficult to classify the species and varieties of amaryllis. Because of the way plant improvement has developed in ornamental horticulture and the lack of records, it is impossible to trace the ancestry of the heterogeneous and hybrid varieties of today.

A. Worsley, writing in the Gardeners' Chronicle in 1901, stated that in his opinion a botanical classification of all the modern amaryllis varieties would divide them into but two species. *Hippeastrum vittatum* remains fundamentally as it existed 100 years ago, allowing for the superiority it has attained through selection and good culture. The other species is more difficult to trace because so many of the original characters have been lost in breeding. The type as it is now known has a short, well-expanded, large, substantial flower with wide segments and the hairy throat of *H. equestre major* Herb., the color of *H. equestre* Herb. and *H. rutilum* Herb. (rarely of *H. aulicum* Herb.), and the keel markings of *H. reginae*. The colors are now very varied. The rarer colors, especially the coppery reds and those nearest white, have of late been diligently sought and selected, and hence have increased in collections, at the expense of other colors.

It is Worsley's belief that the frequent self-colors that appear in lots of seedlings are reversions to some ancestral type, and that the first parents of all our parti-colored or marked flowers were selfs, and inconspicuously colored at that.

The confusion in the genealogy of the amaryllis goes so far as to shadow the parentage of the first recorded hybrid made by Johnson. This variety is recorded in Mrs. Bury's work published in 1831 as the progeny of *Hippeastrum formosissima* × *vittatum*. According to J. G. Baker's Handbook of the Amaryllideae, published in 1888, however, *H. johnsoni* was raised out of *H. reginae* × *vittatum*. To Worsley both these suppositions seem untenable, for he has never been able to hybridize *H. vittatum*, and further he states that *H. johnsoni* does not bear any resemblance to *H. vittatum*. Further to complicate this matter there appear to be two distinctly different plants in the literature, both under the name *H. johnsoni*. Thus down through the list of hybrids there are many discrepancies, resulting in confusion in any attempts to trace the parentage of modern amaryllis varieties. Published descriptions frequently giving incomplete information have sometimes served further to obscure the genealogy of amaryllis.

Also to be considered is the question of sterility in hybrids. In the past doubtless many excellent but sterile hybrid amaryllis have been lost because of an incomplete knowledge of means of vegetative propagation. Fortunately the work of Ida Luyten in the Netherlands in 1926 has clarified many problems in connection with the multiplication of bulbs by asexual means.

Worsley, who is known as the dean of the amaryllis fraternity, stated in 1901 that although his efforts had been directed for many years to producing *Hippeastrum* species hybrids, he could not claim to have met with success in a single instance. He said that he was aware of but three or four undoubted species hybrids—*H. solandriflorum* × *johnsoni; H. johnsoni* × *solandriflorum; H. pardinum* × *reticulatum;* and possibly *H. reticulatum* × *vittatum*. These must be reduced to two or three if *H. johnsoni* is itself regarded as a species hybrid. He acknowledged that other species hybrids have probably been raised and the parentage left in doubt, for such species as *H. equestre, H. aulicum,* and the *rutilium-reginae* group are all good seed bearers when self-pollinated or when crossed with certain hybrid forms. The fact that such hybrids already have the blood of these species, he believed, accounts for the ease with which they cross back with their purebred relations.

Despite the uncertainty enshrouding the lineage of many of the varieties of modern amaryllis, breeding and selection have gone on apace, and each year more interest is being manifested in the development of this flower. In 1934 the American Amaryllis Society was launched. In its constitution its aims are stated as "the promotion of sub-order I Amarylleae, and sub-order II Alstroemerieae, order Amaryllideae." As part of its activities this organization publishes a yearbook, in which is attempted a complete inventory of all Amarylleae as well as the collecting of information from all over the world on the breeding and culture of these plants. It will contain systematic descriptions of new varieties, which will be of tremendous importance both historically and as an aid in breeding work in the future.

The American Amaryllis Society is also sponsoring national amaryllis shows, the first of which was held at Orlando, Fla., in April 1934, with 10,000 blooms. The varieties that attracted most attention were

those having blossoms of pure white or a refined shade of red. The display of amaryllis bearing yellow blossoms was not of good quality, and more breeding and selection are necessary before a pure yellow blossom can be secured.

In 1935 the second national amaryllis show was held at Montebello, Calif. The hybrid types of amaryllis exhibited by commercial plant breeders in California were the outstanding feature of this exhibition. Apparently, striking, clear colors and large sized blossoms were the characters that appealed most to the spectators at this show.

The national amaryllis show was held again in Orlando in 1936. The varieties of amaryllis of Dutch origin were the outstanding display of the exhibition. Perfection of form and color were the outstanding qualities of these varieties.

In the Bureau of Plant Industry, breeding and selection work with amaryllis have been conducted since 1909. The aims in this work have been to improve existing types of amaryllis and to obtain new colors, more shades, and a further increase in the size of the flowers, and in numbers of flowers in clusters. In 1909, 12 varieties of amaryllis were imported—Diana, Venus, Serapis, Progress, Achilles, Crimson King, Vesta, Virgin Queen, Monarch, Bacchus, Adonis, and Scarlet King. The colors ranged from dark red through pink to white with red stripes.

The late E. M. Byrnes, formerly superintendent of the Department greenhouses, undertook by cross-pollination to develop new colors from the original flowers. In 2 years' time the plants resulting from the crosses came into flower. Each year since 1909 this process of selection and cross-pollination has gone on in order to produce superior varieties.

One of the outstanding varieties of amaryllis developed at the Department greenhouses is a pure white one. This was first exhibited in 1920. Since that time this variety has been further improved in size, form, and purity of color.

Each year an amaryllis exhibition is held at the Department greenhouses. Most interest at these shows seems to be directed to the pure white flowers and those of clear, new colors. The larger flowers likewise attract much attention.

The literature fails to reveal any great amount of work on the breeding of amaryllis on the basis of our present knowledge of genetics and cytology. The fact that we have a number of supposed cases of generic hybrids in the Amaryllidaceae has created considerable interest, but it remains to be decided in some of these cases whether the botanical classification of genera has been sufficiently rigid and whether such hybrids actually are the result of crossing two distinct genera.

It is certain that cytogenetic study will be the means of elevating the breeding of amaryllis to a higher plane and of broadening its scope. One of the first steps in such a plan is to acquire and make chromosome studies of as many species as can be secured. As a result of these studies much can be learned concerning the probable parentage of some of our modern varieties. Again, cytological and anatomical studies may solve problems of apparent sterility between certain species. Chromosome studies will be of considerable help in fundamental taxonomic studies of the entire family Amaryllidaceae.

Because the amaryllis varieties are extremely heterozygous, or hybrid, in their genetic make-up, and because they can be propagated by vegetative means, it is questionable whether it is worth while to breed pure-line material that is homozygous. The time element must be considered, for with the amaryllis it takes 2 years from seed to flower while in some of the other genera of the Amaryllidaceae the time is much longer.

For the next decade it is probable that most new varieties will be derived from the hybrid kinds that now exist. However, considerably more thought and effort will doubtless be directed to careful and systematic breeding as the tools and methods of modern plant breeding become better known.

CHINA-ASTER

In popularity the China-aster (*Callistephus chinensis* (L.) Nees) is not exceeded by any other cut-flower annual with the possible exception of the earlier blooming sweet pea. The size, boldness, and attractive form of the blooms, and the sturdy stems and free-flowering habit, as well as the diversity of types available, contribute to its popularity.

A single species, native to China, is included in the genus *Callistephus*, yet this has given rise to a range of forms equaled by few of the garden flowers of today. The family Compositae includes this genus as well as *Aster*, the latter with a great diversity of species, and distinct from China-asters.

A Jesuit missionary, R. P. d'Incarville, introduced the China-aster into Europe in 1731. The original form was single, with two to four rows of ray florets of red, blue, violet, or white, and numerous yellow disk florets. The original stature was medium tall, some 18 to 24 inches in height. The "single chinensis" type now offered by seedsmen and thought to be the old original aster is a midseason type, flowering toward the end of August. Early improvement work was concentrated in France and yielded double forms such as the peony-flowered type. During the first half of the nineteenth century German breeders were so active, chiefly with quilled types, that *Callistephus* became known in America as the German aster. Double forms reached England by 1752, and a variegated blue and white type was known in 1807. By 1851 the quilled type, perfected in Germany, was well known, and dwarf types were appearing. The Comet type, dwarf and compact with lone flat rays and a loose flower head, was introduced about 1886. The Queen of the Market type, notably early flowering with wide-spreading habit and long stems adapted to cutting, appeared in the trade about 1886 from France, where it was already well known in the Paris markets. The Semple strain, tall and strong, with stiff stems and large flower heads, was developed in Pennsylvania. Other tall branching types, emphasizing strong flower stems and large size of bloom, have been developed in the United States for the florists' cut-flower requirements. Recent improvement has been accomplished chiefly by seedsmen, although the Wisconsin Agricultural Experiment Station has taken a leading part in the development of strains resistant to the fusarium wilt disease.

It is generally admitted that a satisfactory classification of China-asters, including all the forms offered by seedsmen today, is imprac-

ticable. Bailey in 1895 offered a tentative classification based on form of bloom and of florets. Beal has offered a more inclusive classification, using four classes of plant habit (tall pyramidal, tall branching, dwarf, single) with further subdivisions based on form of flower heads and florets. Seedsmen also employ the purpose of the variety in making classifications, as florists' cut-flower types, with stiff stems. One American seedsman offers nearly 200 varieties of China-asters and a European firm offers over 500.

During the last decade increasing prevalence of two diseases, wilt and yellows, threatened to wipe out the China-aster. Losses became so heavy that florists and home gardeners alike were turning to other flowers for summer and early-fall cutting, and seed sales dropped alarmingly. Partial control of both diseases has been effected as the result of recent research, in which the Wisconsin station has assumed a leading role. The wilt disease, which is caused by a soil- and seed-borne fungus of the genus *Fusarium*, has been conquered by selection of strains resistant to infection. Yellows, a virus disease spread by a species of leafhopper, may be avoided by growing plants under special cloth shelters, which exclude the insect carrier.

Jones and Riker (*274*) began selection of wilt-resistant asters in 1925. Commercial varieties were grown in "aster-sick" soil, thoroughly contaminated with *Fusarium* as a result of repeated aster culture. No one of the commercial varieties proved to be uniformly resistant to wilt, but resistant individuals appeared among most of the types tested. Selection was continued in the progeny of resistant plants through 1930. Beginning with 1929, extensive testing and selection were carried out at the Bodger Seed Co. farms at El Monte, Calif. Earlier efforts were concentrated on several flower colors in the American Branching group and on the Heart of France variety, but later study has shown that resistant lines are available within other desirable types of asters such as the Semple, American Beauty, Comet, and Royal types. Seedsmen now advertise resistant asters of all major groups except the pompons. Commercial resistant strains, maintained by selection each year, are rarely 100-percent resistant, but represent a marked advance over the unselected varieties.

In the reports on development and improvement of China-asters no mention of artificial hybridization has been found. Furthermore, the genetics of *Callistephus* seems to have been wholly ignored except for one record of an apparent mutant defect in the ray florets of a single form. All the characteristics we have in *Callistephus* today—diverse plant form and stature, divergent form and color of bloom, varying dates of maturity, resistance and susceptibility to wilt—have evidently arisen from the old original type of the species by spontaneous mutation and chance hybridization. All that man has done to improve the aster consists in growing it in immense numbers and in saving those segregates and mutants that have appealed to him as desirable.

The complete range of color now available was obtained years ago. Improvement since the early days has taken place chiefly in form of flower (fig. 16) and in plant habit. The ordinary procedure consists in saving seeds of natural variants, usually produced without protection against crossing with neighboring varieties. After a few years of
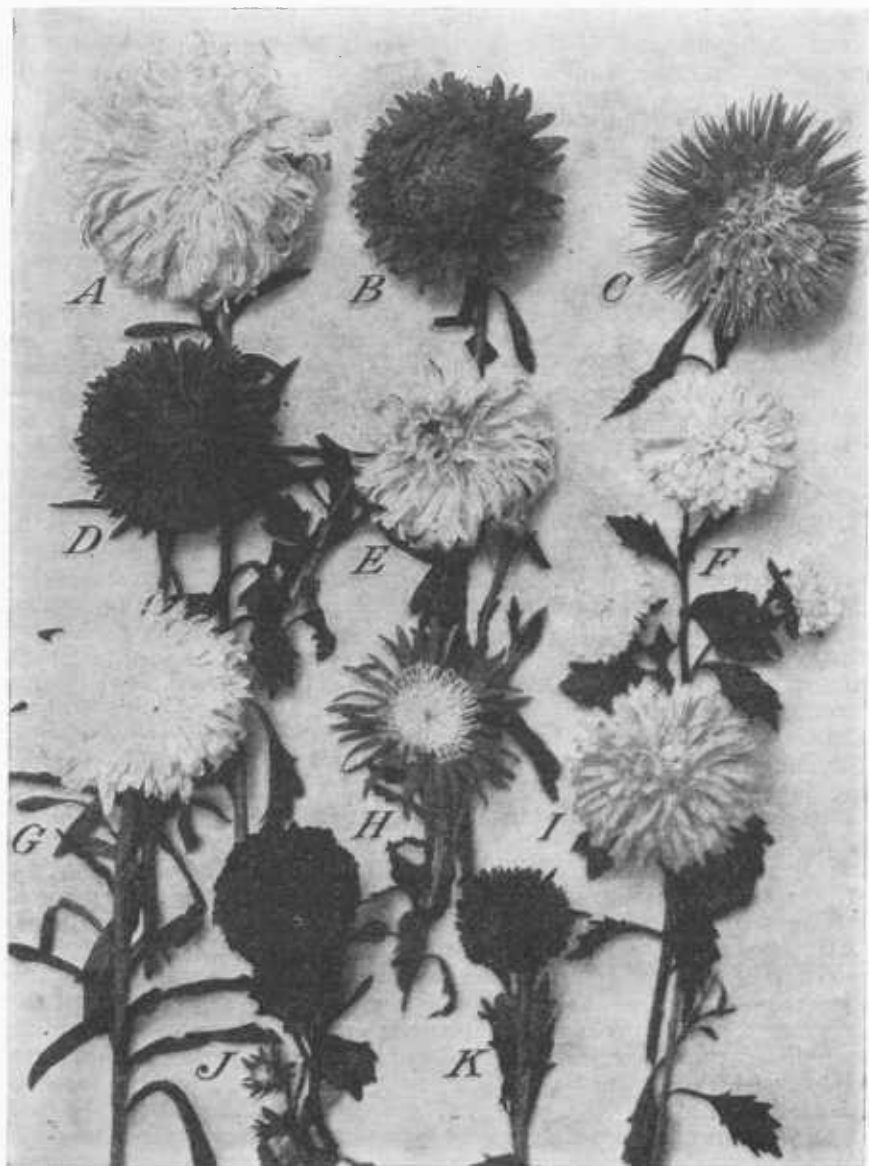
Figure 16.—A few of the many forms of asters now available: *A*, Mammoth or Giant of California; *B*, Early or Late Beauty; *C*, Unicorn or Ray; *D*, King; *E*, Ostrich Plume; *F*, Queen of the Market; *G*, American Branching; *H*, Sunshine; *I*, Hohenzollern; *J*, Victoria; *K*, Tres Naive.

selection the type becomes fixed for the new character, with color variants still appearing within it. Colors are in turn fixed by further selection. As an example, the Comet type appeared on the market in

1886 as a pale pink fading to white. Six years later, rose, blue, and pure white Comet types were offered. It is commonly assumed that the percentage of natural crossing in asters is low, but Fleming (*131*) estimated that approximately 10 percent of natural crossing occurred at Summerland, British Columbia. In the earlier Wisconsin work on wilt resistance, individual plant selection was practiced under cages to exclude leafhoppers, which also insured a high degree of self-pollination.

Fleming grew the progeny of rogues in rows adjacent to the commercial strains from which the rogues were derived. From the variation shown by these open-pollinated rogue types in the next generation he presents certain tentative conclusions with respect to color dominance: white is recessive to all or to most colors; purple is dominant to red, and red to white; deep pink is dominant to white.

In future breeding of the China-aster the most important single characteristic to be sought is resistance to yellows. The search for a yellows-resistant type is complicated by the fact that affected plants develop no viable seed; hence a partially resistant type cannot be continued as a line selection. White (*544*) has noted that the Queen of the Market type, although susceptible, appears to be less severely injured by the disease than later sorts. Development of homozygous, or pure, lines by self-pollination will aid materially in segregating desirable qualities and will permit genetic analysis of such characters as color and habit.

CANNA

When cannas were first recognized as suitable for ornamental purposes, they were tall leafy plants with comparatively small flowers and considerable space between nodes. A chronological history shows that *Canna indica* L. was introduced into England by Gerard in 1596. In 1762 Linnaeus listed but three species. Roscoe in 1828 admitted 21 species. Between 1830 and 1850 the younger Bouché, in Berlin, estimated the number of species at 82. Between 1840 and 1865 Année in France developed a race of garden types from *C. nepalensis* Wall. with pollen probably from *C. glauca* L. This hybrid was called *C. annaei* Andre. Dwarfer cannas with larger flowers appeared when a cross was made by Année in 1863 of *C. iridiflora* Ruiz and Pav. with *C. warscewiczi* Dietr.

From this point on, the interest in securing newer and better types increased rapidly, and there were many horticultural forms developed. As tastes for bedding cannas changed, the new varieties entering into commerce were dwarfer and the flowers larger and of higher quality. Because such types had been originally developed as a result of the work of plantsmen in France, the dwarf kinds are known as French, or Crozy, cannas. The latter name is used because many of the superior types were sent out by Crozy and Sisley of Lyons. Vilmorin of Antibes, Lemoine of Nancy, and Maron of Saint-Germain-les-Corbeil have all contributed to the garden canna as we know it today.

More recent than French cannas are the Italian or so-called orchid-flowered types. The latter name is employed because the flowers of these new cannas resemble the flower of an expanded *Cattleya* orchid. These varieties were first developed in Italy by M. Dammann & Co., at San Giovanni a'Teduccio, Naples. The Italian varieties are recorded as crosses of *Canna flaccida* Salisb., a native of the southern

United States, with garden forms and with *C. iridiflora*. They show improvement in the flowers, which have soft flowing margins and superior colors of golden vermilion.

During the latter part of the nineteenth century new canna varieties were being brought into the United States in large numbers. In 1893 Wintzer (*555*), of West Grove, Pa., became interested in the development of new varieties, with the object of improving the strain and developing new and desirable varieties suitable for "our trying climate."

Wintzer was particularly interested in producing a canna with a clear yellow bloom. As a result of continued hybridization and selection he developed the variety Buttercup. It was rather dwarf, early, and a free bloomer, held its flowers well above the foliage, dropped the faded ones, and the blossoms endured the sun without bleaching. Another quality that Wintzer attempted to develop in cannas was the production of rootstocks that would store well during long winters. He developed two pink-flowered varieties, Martha Washington and Betsy Ross, with small, hard rootstocks, a type resistant to decay in storage. Some of Wintzer's best varieties, including the white Mont Blanc, have resulted from using seedlings that were of no merit commercially but carried characters that he wished to introduce into the progeny. It is possible that in another decade the breeding of new canna varieties will be again stimulated and advanced by new practices and techniques.

The varieties of ornamental cannas offered in the trade today represent types that show great improvement over the original botanical species. There was a time about the beginning of the twentieth century when cannas were much in demand for the extensive bedding work that was then the mode in public parks, cemeteries, and other landscaped areas. In an effort to produce new forms and colors, gardeners year after year hybridized plants with desirable characteristics. In the last 20 years the popularity of bedding plants has waned, and consequently, many of the canna varieties have been lost. This makes a reconstruction of the lineage of the remaining varieties more difficult because many of the intermediate types between the true species and the modern complex hybrids have disappeared.

Even earlier, as a result of the mixing of species due to hybridization, there was considerable confusion in regard to the classification of canna varieties and the parentage of the varieties then in the trade. J. G. Baker, in England, writing in the Gardeners' Chronicle in 1893, concluded from a study of the canna literature from every available source, that the least conservative estimate could not give the genus *Canna* more than 16 species, although 90 had been listed previously. Granting that this confusion existed nearly a half century ago, activities of the last 50 years have done little more with canna classification than to aggravate the situation.

In recent years the canna has received attention in the technical field of cytogenetics. Honing (*213*) in the Netherlands, Belling (*46*) in the United States, and Tokugawa and Kuwada (*513*) in Japan have made contributions to the studies of inheritance in the canna. The work of these men contributes knowledge of practical nature, which can be adapted to the development of superior varieties of cannas for ornamental purposes. These studies have pointed out the advantages and shortcomings of triploid varieties in the canna, a type

which is desirable as an ornamental but usually not suitable for further breeding work. More details of the nature of triploid plants can be found in the paragraphs devoted to genetics earlier in this article.

Belling (*45*) in 1921 studied the behavior of homologous chromosomes in a triploid canna. This variety he secured under the name Gladiator. To the horticulturist it was a noteworthy variety, for it was sterile and the flowers, instead of setting seeds, dropped after they had matured and gave way to new blossoms. The production of seeds in ordinary fertile, diploid cannas is a detriment to continued flowering.

In nearly all cases triploid varieties are partially or totally sterile and thus often incapable of hybridization. In the past much time and labor have been expended in fruitless attempts to cross ornamental plants where one or both of the desired parents used were sterile and incapable of contributing to the production of hybrids. The work of Belling on cannas points out limitations and also opportunities in future breeding work with this plant.

Fortunately for the horticulturist, the canna is readily propagated vegetatively; consequently plants with sterile flowers, if worthy of perpetuation, can be increased in this way. Belling did find, however, that most of the 46 clones of cannas that he investigated had the diploid number of chromosomes, which is nine pairs in somatic cells. It would be from varieties of cannas with the normal nine pairs of chromosomes that high interfertility could be expected in connection with the development of new varieties.

Honing, working in the Netherlands, has published a series of papers since 1914, all concerned with technical genetical studies of the canna. He has reported on the inheritance of pigment in stems, leaves, and fruit papillae of *Canna indica*. As a result of crossing *C. indica* with *C. glauca* he obtained a single hybrid plant that in subsequent generations gave progeny that differed widely among different sowings for the factors of red leaf margins, wax layers on the leaves, and the number and color of staminodes. He also made a genic analysis of the inheritance of flower and leaf characters in the cross mentioned above.

At the Tokugawa Biological Institute, Tokyo, Japan, cytological studies were made on some garden varieties of cannas by Yoshichika Tokugawa and Yoshinari Kuwada. A report of their work was published in the Japanese Journal of Botany in 1924. It included a study of the chromosome number of various varieties of garden cannas. They found that there were either 18 (diploid) or 27 (triploid) chromosomes in the varieties coming under their observation.

These cytological studies in Japan also pointed out that the process of meiosis in canna is generally of somewhat abnormal tendency both in the diploid and triploid varieties. This abnormality of division is possibly the cause of some sterility, which is well recognized in certain canna varieties. Finally the work of Tokugawa and Kuwada showed conclusively that the triploid cannas are larger than the diploids with respect to the stomata openings of the leaves, the size of the cells of the epidermis of the staminodia, the thickness of the leaves, and lastly, the size of the entire flowers. It was also noted that the staminodia of the triploid plants not only are larger than those of the diploid plants but also present a desirable delicate wavy appearance

in their surface.   While this Japanese paper is a technical treatise, it serves as a valuable addition to the knowledge that a practical breeder of cannas must have to carry on his work effectively.

CARNATION

The carnation (*Dianthus caryophyllus* L.) is one of the oldest flowers still under cultivation.   It was first mentioned and described in 300 B. C. by a Greek philosopher, Theophrastus.   The original type was a single flower with five petals, measuring about 1 inch in diameter and of a pinkish-mauve color.   It grew wild over much of Europe, and it still existed in Normandy as late as 1874.

In England, during the reign of Queen Elizabeth, William Turner published an extensive description of this flower.   By this time the double form had made its appearance and already existed in a wide range of colors.   Just when or how the double form arose will probably remain an unsolved mystery.   The flower was very popular in England, and early in the eighteenth century it was used in a successful cross with sweet-william.   Most of the early selection work was done by English amateurs, who rapidly developed a wide range of forms and colors.   They were interested both in the outdoor garden types and in the large, double-flowered varieties of the florists.   In this article the discussion deals almost entirely with the latter type, which is now one of the most important flowers grown under glass in this country.

The florists' carnation occurs in three distinct forms, the single, the double, and the superdouble, or bullhead.   The second type includes all the commercial varieties.   The bullheads are so extremely double that the calyx splits badly as the flower expands.   The first published report that threw some light on the question of inheritance of doubleness appeared as an abstract in the 1904 Proceedings of the American Society for Horticultural Science.   At that time Norton (*396*), of the Department of Agriculture, told of some experiments he was carrying on in the breeding of carnations.   He reported that from the seed of individual capsules he secured all three types of carnation flowers. From one there were 6 doubles (bullheads), 15 semidoubles (commercials), and 7 singles; from another 74 doubles, 147 semidoubles, and 52 singles.   These proportions are approximately 1 to 2 to 1, and they agree fully with what is expected in the progeny from a hybrid when one of the two genes affecting the same character is not fully dominant to the other.   At that time Norton suggested that the practical florist should cross the single with the extreme double type and thus secure a greater proportion of intermediate true florists' types.   The common practice, which still persists, was to cross two commercial double varieties, and always a large proportion of resulting seedlings were singles and bullheads.

In 1907, at the meeting of the American Breeders' Association, Norton (*397*) reported that several crosses between singles and extreme doubles, made in 1905–06, yielded 250 seedlings, which were, with one exception, commercial doubles.   Since no protection from outside pollen was used, the one single seedling may have been an outcross. It was pointed out that single and very double seedlings were usually discarded no matter how desirable their other characters

might be. By pollinating a good single with the pollen of an extreme double that has some new desirable quality, a complete series of standard double seedlings can be secured, some of which may show the new character.

In 1912 Stuart (*498*) presented a more comprehensive publication on this question. The breeding work, begun at the Vermont Agricultural Experiment Station, was completed at the Arlington Experiment Farm, Arlington, Va., after Stuart joined the staff of the Department. The earlier work of Norton was confirmed and the following facts established: When a single was crossed with a single, all the hybrids were singles; a single crossed with a commercial double gave about 1 single to 1 commercial, but when crossed with a bullhead it gave practically all commercial doubles; when 2 commercial doubles were crossed they gave about 1 single to 3 doubles. Unfortunately the doubles in Stuart's report were not classified as to bullheads and commercial types.

The results were analyzed as follows: (1) The commercial carnation as grown by florists is an unfixed hybrid from a cross between a single and superdouble; (2) the bullhead type is incompletely dominant to the single, and the hybrid resulting from crossing them is the intermediate or so-called commercial double.

Unfortunately, the development of superior double carnations is not so simple as the preceding account seems to indicate. Frequently the investigator is hampered by having abnormal plants appear in his progenies, from which very little or no seed can be secured. According to Connors (*81*) and his associates, who carried on carnation breeding at the New Jersey Agricultural Experiment Station for 15 years, there are many types of carnations with respect to the relative development of pistils and stamens. These types include plants bearing male flowers only, plants with all stamens transformed into petals, and asexual types in which pistils and stamens are rudimentary and nonfunctional. It was possible to further subdivide these groups so that 10 types in all are recognized.

In spite of the many difficulties and the meager information on inheritance in the carnation, a very large number of choice varieties have originated as seedlings. Many florists have devoted considerable space and time to this work. One of the leaders was Ward, who devoted considerable time to the production of better florist types and presented his observations on carnation breeding (*533*). At that time he stated that in raising varieties from hybrid seed very few improvements are produced. He estimated that only about 1 in 1,000 seedlings had any merit, and probably but 1 in 5,000 or 10,000 was a decided advance. He also felt that even this low frequency would decrease rather than increase because of the higher standard that was set from year to year.

The list of seedling varieties is constantly changing as old ones are replaced by newer and better types. It has been the practice of many commercial growers to try out a small number of some of the new ones each year. It may happen that one from New England is very inferior in the Colorado section, and one from Colorado may lack quality in Illinois. This has demonstrated, in this country, that it is necessary to develop varieties for a given locality.

Many carnation varieties originate as bud sports. It is a relatively simple matter to propagate these if desirable. These sudden changes may affect any part of the plant. Sometimes the leaves are broader, or deeper or lighter green, or the plant is dwarfer, more compact, or taller. The flower may be modified as to color, size, length of stem, or structure of petals. Since the flower is of primary importance, bud sports are most likely to be noticed when floral characters are involved.

Unfortunately there is no authentic evidence on the frequency of bud sports in carnations. Isolated observations in various sections of the country seemed to indicate, however, that they might occur at a rather high rate. Unquestionably many of the best of our current varieties arose in that way. As a result growers have become accustomed to keeping a careful watch over their benches during the growing season. Since, under the stress of commercial operations, there is always the possibility of mechanical mixture of rooted cuttings, it is impossible to give an accurate account of the situation.

There are a number of carnation disease problems in the solution of which the plant breeder should be useful. Two of these diseases, carnation rust (*Uromyces caryophyllinus* (Schrank) Wint.) and stem rot (*Corticium vagum* B. and C.) may at times become very troublesome. Varieties resistant to these diseases, provided they were also of high quality, would be very acceptable. There is some evidence that resistance to rust already exists in some of the better commercial varieties. In 1932, a test of 36 varieties was made at the Waltham Field Station, in Massachusetts, and they were grouped for rust resistance as very susceptible, moderately susceptible, slightly susceptible, and resistant. The standards for grading resistance were not stated, nor were the severity and uniformity of the infection given.

The problem of color inheritance has received very little attention as yet. The highly heterozygous conditions of the carnation and the very frequent functional sterilities encountered have discouraged research along these lines. As facilities for flower breeding are increased, it is likely that some attention will be given to these problems.

The condition known as carnation splitting is another problem that should receive more attention from the flower breeder. It was studied by Connors, who stated that it was caused by two conditions— the formation of an unusually large number of petals through transformation of stamens and pistils, and the development and growth of secondary buds within the flower.

As early as 1903, Ward had assumed that splitting was entirely hereditary, and he advised the selection of seedlings that produced flowers with an unsplit calyx. Later, Connors stated that the experience of the New Jersey station indicated splitting was influenced by both hereditary and environmental factors. It is needless to say that a good nonsplitting variety would be a valuable contribution.

Since there is a rather definite regional adaptation of varieties, it seems that a sound carnation breeding program should include facilities for testing all seedlings in as many different locations as possible. When the work is carried on at only one location, there is loss from discarding seedlings that might prove very valuable in another region.

Chrysanthemum

The culture of improved forms of chrysanthemums antedates the beginning of the Christian era by several centuries. Apparently they are native to China, and are mentioned in Chinese literature as early as 500 B. C. The Japanese grew them extensively at an early period and did considerable work in developing improved types. A form with 16 petals was chosen as the flower emblem of the Emperor. In both China and Japan, single-stemmed varieties were generally grown long before the plant was introduced into western Europe.

The earliest record of chrysanthemums in Europe is of an importation in 1688. It seems strange that this attractive flower was not known to Europeans at an earlier period. The following year several varieties were reported as being grown in the Netherlands, but for some unknown reason they soon passed out of cultivation.

It was not until 1764 that chrysanthemums made their appearance in England. They soon became popular, and additional varieties were imported from China in 1789. During the following 20 years, eight new types were introduced from China.

All the early varieties introduced into Europe were brought in as living plants. The first attempts to grow seedlings were not made until about 1827. At this time a Frenchman, M. Bernet, flowered several fine seedlings from seed he found in withered flower heads the previous autumn. Following this it is very probable that many amateurs began to grow seedlings, but unfortunately we have no records of any new developments.

In 1846 Robert Fortune brought two small-flowered varieties from China and introduced them into English gardens. They were not well received by the English, but when sent to France they soon became rather popular and were used extensively in hybridizing. It seems probable they were the progenitors of our modern small-flowered varieties.

The early history of chrysanthemums in the United States is rather obscure. According to the 1828 catalog of William Prince, they were introduced into Hoboken by John Stevens in 1798. The plants were probably a dark purple form, which had reached Europe from China in 1790. In 1826 the Prince's Nursery listed 26 varieties, and by 1835, according to Hovey's American Gardener's Magazine and Register, 50 distinct varieties were available in this country.

There is no record of the origin of any of these early chrysanthemums. Propagation by cuttings was very simple, and strains were perpetuated in this way. Undoubtedly this was a strong factor in retarding breeding. The fact that so few different types existed in this country in 1835 is an indication that very little actual improvement by breeding had been attempted.

One of the earliest breeders in this country was Robert Kilvington, of Philadelphia, who exhibited a new seedling named William Penn before the Pennsylvania Horticultural Society in 1841. It was a large white double flower, almost globular in shape. It seems strange that this did not immediately stimulate more work, but no other contributions appeared for some time. About 1850 Samuel Brookes, of Chicago, became very much interested in chrysanthemums and did considerable work to stimulate interest in the flower.

A general interest in chrysanthemums was slow to develop in this country. In 1844 an impressive display was made of many of the available varieties at the fall show of the Massachusetts Horticultural Society. Two years later there was a large exhibit before the Pennsylvania Horticultural Society, where the chrysanthemum was described as the coming flower. A special chrysanthemum show was not held, however, until 1868. At present there are many chrysanthemum exhibits each year.

Previous to 1850, chrysanthemums were not grown as greenhouse plants. About this time a few varieties were tried under glass, and development of special florists' types was soon under way. The development of this branch of the florists' business soon extended the blooming period and made it possible to market the large showy types that were being introduced from Japan. About 1883, Hosea Waterer imported about 50 varieties from Japan. Shortly following this, a large white variety appeared that was so attractive it is said to have been sold for a fabulous sum. This variety was sent to Mr. and Mrs. Alpheus Hardy by an appreciative friend in Japan. It was named Mrs. Alpheus Hardy and undoubtedly was one of the stimulating influences that led to a quickening of interest in chrysanthemum breeding in this country. Some of the successful breeders of this period were T. H. Spaulding, E. Fewkes, Pitcher & Manda, V. H. Hallock, W. C. Pyfer, E. G. Hill, and F. Dorner & Son. By 1894, there were listed 163 varieties of American origin.

In the latter years of the past century, one of the most prolific of modern chrysanthemum breeders, Elmer D. Smith, of Adrian, Mich., began his work. He had introduced 445 new varieties by 1928, and many others have been added since that time. Other American breeders who contributed many new chrysanthemums during this period are E. M. and J. W. Byrnes and F. L. Mulford, of the Department of Agriculture. More recent entrants in the work have been V. R. De Petris, of Detroit, Mich., and Alex Cumming, Jr., of Bristol, Conn., who has specialized with outdoor chrysanthemums.

The efforts of these breeders have been mainly to develop greenhouse or so-called forcing chrysanthemums. A program to develop hardy outdoor types has been under way in the Department for some time. The work was started by growing outdoors as extensive a collection of varieties as possible, and securing data on their time of bloom and winter hardiness. The work was carried on at first at the Arlington Experiment Farm, but in recent years certain selections have been sent to various cooperating State experiment stations for trial. By selecting each year the earlier flowering types and growing seedlings from them, races have been developed that bloom as early as July in the vicinity of Washington, D. C. (fig. 17). The earliest strains are followed successively by others until heavy frosts kill the plants. The work has demonstrated very clearly that time of bloom is actually a hereditary trait transmitted from parents to seedlings.

The problems involved in chrysanthemum breeding are to some extent very similar to those faced by the rose breeder. The history of the early chrysanthemum varieties is not known, but it seems likely that most of them arose as mutations or bud sports from other varieties. While there are no data on this point, the evidence all points in

that direction. So far as can be determined, little or no breeding work was attempted in China or Japan, and all varieties were maintained by the rooting of cuttings. If a new color or other bud sport appeared, it was simply increased by cuttings and soon became established. Had the Japanese and Chinese been growing seedlings there would certainly have been many more varieties available in

Figure 17.—The chrysanthemum breeding plot at the United States Horticultural Station, Beltsville, Md., where hardy early-blooming varieties are being developed. Already a wide range of types and colors have been developed, and the blooming date continues from late July to killing frosts. In the background are cages built over 8 plants to protect them from cross-pollination.

those countries when the flower was first brought to Europe. This point is strikingly confirmed by the fact that Smith was able to develop over 450 new seedling varieties in a little over 30 years. Some of these may have been bud sports, but by far the larger number were seedlings.

The keeping of parentage records has been fairly thoroughly done by some breeders. Since the modern chrysanthemum is really of rather recent origin, and probably does not involve a very complex mixture of species, such records should have some value. If they all were available it seems very likely they would show that certain parents produce more good seedlings than others. While there is little or no scientific data on the inheritance of plant characters in chrysanthemums, breeders have learned through experience that certain varieties are likely to transmit their flower color. The variety Harvard, for example, usually produces red seedlings in crosses, and Thanksgiving Pink transmits its pink color. These observations seem

to indicate a probable dominance of these colors over other shades, and also that these varieties may be pure for their respective colors.

One of the greatest difficulties encountered by the chrysanthemum breeder is the failure of many fine varieties to set much seed. In some instances this may be due to an actual sterility, but it is generally the result of the extreme doubleness of the flower. Not much can be done about this unless a single can be found, which when crossed with a double gives all double seedlings. Under such conditions, all crosses could be made with the single as maternal parent.

The production of bud sports or mutations has also played a rather important role in the development of the chrysanthemum. The mutation tendency is undoubtedly higher in some varieties than in others. In the absence of any scientific data we are forced to rely on general observations as to the frequency of such changes. According to some growers, the sport of a variety very frequently reverts to the parent type. The mutations that have been observed are mostly flower color changes. Very probably there are others affecting foliage and other characters.

. The possible causes underlying the sudden appearances of bud sports are mentioned in another section of this article. If more were known about them we might be able to produce controlled mutations in greater numbers. If they result from some environmental influence, then varieties of chrysanthemum must differ markedly in their response to it, because some varieties mutate more readily than others. This indicates an inherent mutation tendency. In other words, chrysanthemums may have some rather unstable characters and may mutate under certain environmental conditions.

DAHLIA

Francisco Hernandez, physician to Philip II of Spain, was sent on an expedition to New Spain (Mexico) in 1570. The purpose of this journey into the New World was to study the natural history of this intriguing land to the westward. After Hernandez returned to Spain he published in 1615 four books on the plants and animals of Mexico. In one of these books he described three types of plants which nearly 200 years later were to be called dahlias. To these three plants he gave the Aztec names acocotli, cocoxochitl, and acocoxochitl, which mean, respectively, "water pipe", "hollow-stem flower", and "water-pipe flower", the allusion being to the hollow stems of the plants.

From Hernandez's writings it is apparent that the Aztecs had worked on the improvement of these plants, for this report indicates that they varied in color, form, and degree of doubleness. The illustrations he published show that somewhat double dahlia flowers existed in Mexico in the sixteenth century.

Vitalis Mascardi in 1651 published a work in Rome in which there is an illustration of a double-flowered dahlia. Again, in 1787, a Frenchman, Nicholas Joseph Thiery de Menonville, searching in North America for the valued cochineal bug, described dahlias, growing in a garden near Oaxaca, which had large asterlike flowers, stems as tall as a man, and leaves like those of an elder tree.

It was not until after 1789, however, that the Old World awakened to the possibilities of the dahlia as an ornamental plant. In this year

Vincente Cervantes, director of the Mexican Botanic Gardens, sent to the Royal Gardens in Madrid seed of dahlias from Mexico which were destined to play a tremendous part in the development of the superior types of garden dahlias as we know them today. It was to Abbe Cavanilles, director of the Royal Gardens, that these seed were sent, and from them were produced flowers of brilliant hues typical of the dahlias to be found growing in Mexico.

Cavanilles named this plant, which was practically unknown in Europe, Dahlia, after Andreas Dahl, an eminent Swedish botanist living in Berlin, who had been a pupil of the great Linnaeus. Among the plants that Cavanilles received from Mexico he recognized two species, *Dahlia pinnata* Cav. and *D. coccinea* Cav. The former, which showed great variation in its progeny, has since been called *D. variabilis* Desf. and *D. rosea* Cav., but according to the rules of botanical nomenclature the name *D. pinnata* must stand. *D. coccinea* does not cross readily with other species, and its flower color is confined to scarlet and shades of orange.

At the time Cavanilles received the shipment of dahlias from Mexico a great deal of interest was being manifested by botanists and plants-men of Europe in plants from the New World. Within a few years seeds of the dahlia were sent to a number of botanic and private gardens in Europe. In 1798 seeds were sent to Kew Gardens in England, but apparently plants from the seeds died before they reached maturity. By 1803 an English plantsman had flowered *Dahlia coccinea*, for in Curtis' Botanical Magazine of 1804 appeared a colored figure with the statement, "Our drawing was taken in June 1803 at Mrs. Fraser's, of Sloane-Square, who has the credit of introducing this ornamental plant among us from France."

From 1804 to 1806, shortly after Alexander von Humboldt sent seed from Mexico to Paris and Berlin, a phenomenal increase in the number of dahlia varieties occurred. Within 12 years nearly every color that we have today had appeared in the flowers. In 1806 the Berlin Botanic Gardens had growing 55 single and semidouble varieties. Two years later the first perfect double dahlia was raised by Hartweg at Karlsruhe, and the year following a variety with single white flowers was developed.

By about 1810 the dahlia became exceedingly popular and growers sought assiduously to improve and create better double flowers within the genus. Both in the British Isles and on the Continent new forms, showing doubleness and brilliant colors, were developed. In the Botanical Magazine for 1817 an illustration revealed a rose-colored dahlia that originated in France and showed the form of the decorative dahlia as the type is now known.

From 1810 to 1850 interest in the dahlia increased tremendously. The ease with which hybrid seed could be secured, because of relatively self-sterile flowers, the short time required to produce new varieties, and the extreme variation secured both in sizes and colors of the flowers all contributed to the popularity of this new plant. Of particular interest in revealing the quality of dahlia varieties of that time is The Annual Dahlia Register for 1836. This contains particulars of the introduction of the dahlia into England and, most important, has as illustrations upward of 50 highly colored figures of dis-

similar dahlias. It also contains an index of 700 varieties of the dahlia that were recognized as such at that time. The illustrations in this book show double flowers exclusively, all with a colorful array of petals in very dense, round heads, arranged very geometrically. It was this stiff, formal, double flower that was so popular in the first half of the nineteenth century, and the type in which interest waned to a marked degree in Europe shortly afterward.

Seed of the modest dahlias that had been sent abroad from North America were returned to their native shores and yielded plants with flowers of an endless array of color patterns and degrees of doubleness. In the United States the craze for new dahlia varieties was nearly as acute as it was in Europe, and likewise, interest in the stiff, formal flower began to wane about 1860.

The first National Dahlia Society was organized in Great Britain in 1870, and about that time the diminutive pompon type of dahlia was developed, but these two events did not serve to recreate any great amount of interest in varieties then existing.

About 1864, however, an event happened that brought renewed interest in the dahlia through the discovery of a species with characters far different from and superior in many ways to those in the dahlia varieties known at that time. One M. J. T. Berg, of the Netherlands, received a collection of plants from Mexico. Included in this shipment was one dahlia root with just sufficient reserve food remaining within it to send up one shoot. In the fall this shoot produced a brilliant, blood-red flower of a shape never before recorded. The quilled petals, typical of the dahlia of that time, were lacking, and in their places were petals that were recurved, with pointed ends. The plant was tall and sturdy and carried its flower well above the foliage.

This new dahlia was given the name *Dahlia juarezii* Hort. in honor of the then President of Mexico. It received the name "cactus dahlia" because of its resemblance in form and color to the blossoms of a cactus. This plant was to play an important part in the development of superior varieties and to become the progenitor of two new classes of dahlias, now collectively referred to as the cactus and hybrid-cactus types. The species reached England and was first illustrated in the Gardeners' Chronicle in 1879.

All efforts to trace the origin of this new dahlia failed until 1916, when Wilson Popenoe discovered the probable ancestral home of *Dahlia juarezii* in Guatemala. The primitive species he found there has a single row of eight long, spreading, crimson rays turning backward along the margin. This species was named *D. popenovi*, and it is believed to be one of the ancestors of *D. juarezii*.

It was fortunate that *Dahlia juarezii* was discovered, for in the latter part of the nineteenth century there was, both in the United States and abroad, a reaction against formalism in all arts. The stiff formal dahlia flowers that had been the rage for the past half century were outmoded. This served as a challenge to the breeders of dahlias, and, having in their possession a new species of dahlia exhibiting characters that were in demand, they began to breed new varieties to suit the public's fancy.

This activity went on for a number of years, and the progeny resulting from crosses with the new-found *Dahlia juarezii* created

great interest, particularly at dahlia exhibitions. The very fact that the flowers were displayed mostly at flower shows, however, ultimately created still another problem for the plant breeder. Interest had been centered chiefly in new and superior blossoms, while the structure of the plant upon which these flowers were borne was neglected. Consequently the new varieties possessed very weak stems and were suitable only for cut-flower exhibition purposes. As interest in outdoor displays developed, breeders were faced .with the task of increasing plant vigor to reach parity with the excellence of flower quality.

Within the last 20 years much has been accomplished in securing superior varieties of dahlias. Varieties having weak short stems have gradually been supplanted by more vigorous types, and breeding has reached a high level. The number of named varieties now existing is well over 7,000, for in 1924 J. B. S. Norton published a book entitled "Seven Thousand Dahlias in Cultivation", and the number has been added to greatly since that time.

Many dahlia societies have been organized in both the United States and Europe and these have stimulated interest in the improvement of dahlia varieties. In the United States the American Dahlia Society has functioned for two decades. One of its outstanding activities is the publication of a quarterly bulletin dealing with all aspects of the culture and breeding of the dahlia. This organization also stimulates interest in the development of superior varieties by conducting flower exhibitions and trial gardens where new varieties are grown, evaluated, and exhibited.

These developments have led to considerable confusion in attempts to classify, especially for exhibition purposes, the various garden types now existing. In an effort to simplify the classification of the host of new varieties that have been developed, the American Dahlia Society had adopted a classification based on the form and size of the flower. Fourteen classes are provided for the systematic arrangement of all the various types of dahlia flowers. A number of these classes are subdivided according to the size of the flower.

Other countries also have their classifications for dahlias. A great deal of pioneer work in this direction was performed by the Royal Horticultural Society and the National Dahlia Society in Great Britain.

Worthy of special comment in considering the development of superior dahlia varieties are the trial grounds where new varieties are grown, studied, and evaluated. The American Dahlia Society has such a garden in cooperation with the Connecticut State College at Storrs. Each year a field day is held at the trial grounds, when new varieties are inspected and evaluated. Competent judges pass on the merits of each new variety, and thus the value of new kinds can be impartially reported to those interested in dahlias. Other trial grounds are conducted by State and regional dahlia organizations; these plots permit the study of the same variety under varied climatic and other environmental factors.

Scientific research has revealed in the dahlia an interesting story of the inheritance of color. In the comparatively new field of cytogenetics, investigations conducted by Lawrence (*310, 311*), curator, the John

Innes Horticultural Institution, Merton, England, are noteworthy. This work indicates how the lineage of dahlia species and varieties can be studied by modern scientific methods. Lawrence found that the colors in all available dahlia species fall into one of two color groups: (1) Pale to deep magenta over ivory-white ground color, and (2) orange to scarlet over yellow ground color. One important exception Lawrence noted was that in the so-called species *Dahlia pinnata*, more popularly known as *D. variabilis*, which is considered the source of most of the garden varieties, the flower color is made up of a combination of both of these color groups. Furthermore, through cytological studies, he found that this same plant has 64 chromosomes in the vegetative cells, or twice the number usually found in species of the dahlia. These two facts indicated that *D. pinnata* is itself a hybrid. Such work, besides aiding the taxonomist in systematizing dahlia nomenclature, is of value to plant breeders in their efforts to produce superior varieties of plants.

Lawrence's work also dispelled the widespread erroneous belief that the extreme variation of *Dahlia pinnata* showed the degree to which a species could vary following domestication. This extreme variation was shown to result from the complex genetic make-up of a hybrid which combined various specific characters brought together during the descent of the genus *Dahlia* from a primeval stock. This coupled with multiplication of chromosome numbers probably accounts for the present variability of the stock.

The dahlia, like many other perennial ornamental plants, is readily propagated vegetatively. As a consequence it is not necessary to develop lines that are pure or homozygous, as is necessary with plants propagated from seed, in order to perpetuate the same characters in subsequent generations. Ease of vegetative propagation of the dahlia is particularly fortunate because its self-sterility enforces cross-pollination, thereby maintaining a high degree of hybridity in the genus and making pure-line breeding laborious and difficult. Despite these complications, however, the development of reasonably pure-breeding stocks may have to be undertaken in the future by plant breeders, not so much in order to produce dahlias of superior ornamental value as to develop types resistant to or immune from plant pests.

GLADIOLUS

The superior varieties of gladioli grown today have been developed largely through work that began scarcely more than a century ago. It may be assumed from ancient writings that the Greeks and Romans made use of native gladiolus species for ornamentation, and it is certain that there were species of the gladiolus, known as Corne Flags, in Britain as early as 1597, when they were recognized as important garden plants by Gerarde. But it was not until 226 years later that the first important hybrid gladiolus was produced.

Interest in Europe was at first limited to the species native to southern Europe, Asia, and Persia. They numbered but 15 and were never very popular with gardeners. Early in the seventeenth century the development of these species came to a standstill. It was more than a century later, when new species first started coming in from southern Africa, that renewed interest was gradually stimulated in the gladiolus.

In the eighteenth century botanists and explorers became increasingly aware of the new species of plants to be found around the Cape region of Africa, but it was not until the close of that century, when the Cape of Good Hope became subject to Great Britain, that large importations to Europe were received. William Herbert, dean of Manchester, seems to have been one of the first to recognize the value of the Cape species of gladioli, for in 1820 he wrote:

I am persuaded that the African Gladioli will become great favorites with florists, when their beauty in the open border, the facility of their culture, and the endless variety which may be produced from seed by blending the several species are fully known, nor will they be found to yield in beauty to the Tulip and Ranunculus.

Dean Herbert, besides contributing valuable information to horticultural literature, was also an enthusiastic cultivator of gladioli and was regarded as an authority on Cape bulbs. He carried on considerable hybridization with the species of gladioli and recorded in the horticultural literature a large number of his successful crosses.

During Dean Herbert's time the first important hybrid appeared at Colville's Nursery, Chelsea, England, in 1823. It was derived from *Gladiolus tristis* L. var. *concolor*, with *G. cardinalis* Curt. as the pollen parent. This new variety was given the Latin name *Gladiolus colvillei* Sweet and was known commonly as Colville's corn flag. It was described as being tall and vigorous with flowers of bright scarlet with lanceolate blotches of white on the three lower petals. There are to-day several named varieties persisting in the trade that came directly from this outstanding hybrid. In the United States they are generally grown under glass in the East but will grow out of doors successfully in the milder climates along the west coast.

Fifteen years later the second important hybrid, which was named *Gladiolus ramosus* Paxt., was produced in France. It was first flowered by M. Rifkogel in 1838. Records indicate that this hybrid resulted from a cross between hybrids of *G. cardinalis* and *G. oppositiflorus* Herb. It bore a tall flower spike with heavy broad leaves. The flower was openly funnel-shaped and bright red with deep blotches at the bases of the three lower segments. The fact that it bloomed later than other varieties of its time made it important for at least the next 20 years.

Until 1841 there was a mild yet increasing interest in gladioli, particularly among amateurs, but that year a variety was introduced that caused the greatest stimulation ever evidenced in the history of gladiolus breeding. M. Beddinghaus, gardener to the Duke of Aremberg, had been breeding gladioli for a number of years, securing for this work as many species as were then available. Louis van Houtte, of Ghent, Belgium, realizing the potentialities of one of M. Beddinghaus' productions, immediately purchased the stock, and in 1841 *Gladiolus gandavensis* Van Houtte was introduced to the world. Van Houtte named this gladiolus after the city of Ghent and described it in glowing terms as bearing majestic flowers, numbering 18 to 20, of the most charming vermilion, the inferior petals adorned with chrome, amaranth, and brown. For a long time there was considerable controversy concerning the parentage of *G. gandavensis*. It is now accepted that this new variety resulted from a cross between *G. psittacinus* Hook.

and *G. oppositiflorus* or between hybrids from these species. Napoleon III heard of this variety, which had "created a furor in the gladiolus world", and some of the plants came into the possession of Souchet, gardener to the Emperor at the court of Fontainebleau. Souchet, using *G. gandavensis* as one of the parents, developed many new hybrids, which in time were the talk of Europe.

In England Dean Herbert kept in close touch with new gladiolus varieties and continued the pioneer work he had started, using new species and varieties in his breeding work as they became available. Representing the trade in England, James Kelway, the founder of the Langport firm, was alert to the rapid development of the gladiolus and secured hybrids from Souchet in France to develop them further and make them available for sale in England.

Queen Victoria's visit to Fontainebleau in 1855 is reputed to have stimulated a tremendous interest in the gladiolus, for she saw and greatly admired the new varieties developed by Souchet and exhibited by Napoleon III. By 1880 over 2,000 named varieties had been developed that showed characters derived from *Gladiolus gandavensis*.

Victor Lemoine was greatly interested in the development of new gladiolus varieties and the next race of hybrids of considerable importance resulted from his work at Nancy, France, around 1880. Crossing *Gladiolus gandavensis* with *G. purpureo-auratus* Hook., which was introduced in 1872, he obtained a race called *G. lemoinei* Hort. These varieties were characterized by their large flowers and the prominent blotches in the throat of the florets.

Meanwhile Max Leichtlin, of Baden-Baden, Germany, crossed *Gladiolus gandavensis* with *G. saundersii* Hook. f., which had been introduced from the Cape in 1870, and *G. leichtlinii* Baker was produced. This stock was ultimately purchased and imported by John Lewis Childs, of Long Island, N. Y., and renamed *G. childsii*. W. Van Fleet crossed a variety of *G. childsii* with *G. cruentus* Moore and secured, among many others, his famous variety Princeps. The *purpureo-auratus-gandavensis* hybrids developed by Lemoine were crossed by him with *G. saundersii* and a new race called *G. nanceianus* Hort. resulted, which was characterized by plants having remarkably large, open flowers with contrasting color mottlings in the throats.

Gladiolus primulinus Baker has been the most recent introduction to greatly influence the development of gladiolus varieties. This species was found in the Rain Forest near Victoria Falls on the Zambezi River in Africa. It was successfully introduced and flowered at Kew Gardens, England, in 1890. Since then it has played an important role in modifying gladiolus flower form and color. French, English, and American plant breeders have all taken part in developing new varieties with some of the characters of *G. primulinus*. The most outstanding characters it transmits are a light and graceful flower stem, a more or less pronounced hooding of the flowers, and a subduing of brilliant hues to soft pleasing colors. In turn the progeny from *G. primulinus* have been improved by increased flower size and more vigor in the flower stem.

Noteworthy also are the ruffled gladioli, which have been developed in the United States by A. E. Kunderd, at Goshen, Ind., starting about 1907. Later he also developed a strain having fringed and laciniated

segments, which has created much interest. Foremost among the Canadian pioneers in the development of the gladiolus was the late H. H. Groff, of Simcoe, Ontario. About the end of the nineteenth century he had developed a strain called Groff's hybrids, which were considered noteworthy, particularly because of the wide range of color they possessed.

At the present time there are many amateurs and professional and commercial growers deeply interested in the breeding of new and superior varieties of gladioli in the United States. The American Gladiolus Society, organized in 1910, did a great deal to encourage the production of new and finer varieties, as well as to straighten out nomenclature. It publishes a monthly, the Gladiolus Review, in which registrations of new gladiolus varieties are included. This organization sponsors affiliated State and regional societies and conducts an annual gladiolus show where new varieties are exhibited and evaluated.

Governmental agencies have also contributed to the development of the gladiolus. Particularly noteworthy is a series of publications during the last 20 years from the New York State College of Agriculture, Cornell University, by A. C. Beal, A. C. Hottes, and A. M. S. Pridham of that institution on the development of superior varieties of gladioli. At Cornell University there is a test garden in which most of the available species and varieties of gladiolus have been grown and studied. Likewise, at the New York Botanical Gardens a collection of gladiolus species is maintained.

Recently a technical paper has appeared written by Bamford (*10*), of the Maryland Agricultural Experiment Station, who collected many gladiolus species and varieties and made detailed chromosome counts. His work greatly expands similar studies on the same subject by M. Ernst-Schwarzenbach (1931) in France and by McLean (*326*) in the United States. Such cytological studies are of great help to the geneticist in his attempts to classify material and breed superior varieties.

This brief discussion serves to direct attention to the great complexity of the inheritance of modern gladiolus varieties. Original species have been combined and hybrids have been crossed and recrossed until the resulting multiple hybrids possess characters derived from many different species. Superior characters have been combined and varieties have been selected covering a wide range of usefulness, from the requirements of the florist who forces plants under greenhouse conditions to those of the amateur flower lover who demands a wide range of color and form for flowering through the summer.

How much more can be accomplished in the development of the gladiolus is a matter of speculation. When it is realized, however, that less than a score of the more than 150 known species have been used to any extent in the development of over 2,500 varieties of gladiolus in commerce at the present time, it seems probable that present and future plant breeders can still draw from the remaining species to give to the world even more desirable gladioli than we now enjoy.

HEMEROCALLIS (DAYLILY)

The daylilies had not received much attention from breeders until the last decade of the past century. Previous to this a few species had been grown in Europe. They were first mentioned by Pena and

Lobel in 1570, when these authors described what is probably the common Lemon daylily. A few years later Lobel described a second species with single cinnabar-red flowers. These two were apparently the only ones known in Europe for the next 200 years. Unfortunately little is known of the situation in China and Japan before the nineteenth century.

In 1768 a third type was mentioned in Europe, but its exact origin is unknown. It was regarded by some as being a minor variety of one of the two older established types. About 1798 another new type appeared, this time imported from the Orient into England. No new ones were introduced until about 1934, when a semidwarf form was brought in from Japan. In 1856 another semidwarf appeared, and this was followed in 1860 to 1864 by double-flowered forms.

The first actual breeding of daylilies probably dates from about 1890. Previous to this all new types that had appeared in Europe and the United States were simply plant importations from the Orient. The development of new types from seedlings was begun about 1890 by George Yeld in England. His first introduction, named Apricot, appeared in 1892. A more recent contributor is A. B. Stout, of the New York Botanical Garden. He has attacked the breeding problem from a scientific angle, and it is to him that we owe the greatest part of the genetic information now available on this group of plants. The breeding of new forms has increased so rapidly, chiefly as a result of his research, that there are now probably more than 300 different varieties.

The breeding of daylilies is handicapped by many obstacles. Among these are self-sterility and cross-sterility, which inhibit seed setting, the hybrid nature of the available types, and the comparatively slow rate of increase after a desirable variety has been developed.

The types of sterility encountered may, according to Stout, be classified into four groups:

(1) There appears to be lack of affinity between certain species in the relations of fertilization. Yet hybrids have been obtained from many of the combinations between species.

(2) There is much abortion of pollen grains and egg cells in certain hybrids, such as *Hemerocallis flava* L. × *H. nana*, and in triploids, such as the Europa daylily. This condition greatly reduces the chance that a plant will bear seeds, but there may be a few viable pollen grains, in which case the plant may be used as a pollen parent.

(3) There is abortion of pistils in the older triploid double-flowered forms, although some viable pollen is formed.

(4) In daylilies there are many types of incompatibility. Some plants set seed only when self-pollinated, others when pollinated by sister plants, and still others only when cross-pollinated by certain other species. Studies have been made which show that in some cases of sterility pollen tubes grow poorly in the style or fail to enter the ovary. Some clones are completely self-sterile, others set a few seeds when self-pollinated.

The wide variation in any group of daylily seedlings is rather striking. Even seedlings of the older, well-established clones are usually very inferior to the parent type. This indicates, of course, that daylilies are probably heterozygous for a large number of genes. The chances of securing improved types depend almost entirely on the

number of seedlings grown. According to Stout, only 14 superior seedlings were found out of a total of 15,000 grown. Others apparently had some merit, since about 100 more were saved for use in selective breeding.

The present information on daylilies indicates that many new types can be developed by intercrossing the existing clones. Because of the heterozygous nature of the material, lack of genetic data, and general self-sterility, a scientifically planned breeding attack is difficult. About all that can be done at present is to grow large populations and select the superior types either for introduction or further breeding. It would be desirable to establish some self-fertile lines so that a genetic analysis of some plant characters could be made.

The cytological investigations of daylilies have shown some interesting results. The basic chromosome number of all the species appears to be 11. The common European form of *Hemerocallis fulva* L., which Stout calls Europa, has 33 chromosomes and is therefore a triploid. According to Belling and Stout this species shows considerable irregularity in the formation of pollen cells, so that very few good pollen grains or egg cells are formed. Further studies by Stout showed that triploidy was fairly common in daylilies and this may account for some of the prevalent sterility.

IRIS

The garden irises may be grouped in several classes, such as the bearded, beardless, and bulbous types. This discussion is limited to the commonly cultivated tall bearded type. As is true of many other ornamental plants, the early history of the iris is shrouded in mystery. According to J. C. Wister, bearded irises are native to central and southern Europe and Asia Minor, in a region extending from the Alps through Italy, Hungary, Bulgaria, Palestine, and Iraq. There are no records of when man first began to cultivate the wild types, but it was probably very early, since the ancients attributed various medicinal properties to the rootstocks.

Iris albicans Lange is the first species about the culture of which there is definite knowledge. This iris probably originated in Arabia and was carried all over southern Europe by the Mohammedans, who planted it on the graves of their soldiers. There are no records as to when this practice was begun, but by 750 A. D., when the Mohammedans were driven out of Spain, the species *albicans* was already well established there.

The first reference to the growing of the iris in European gardens was in 1790. At this time about a dozen wild forms were listed in several garden catalogs. The next 60 years saw a rapid increase in the popularity of irises, and it was during this period that the first iris breeding was begun. Prominent among the early workers were Lemoine, Jacques, and Salter, who produced many new improved forms. Unfortunately there are no authentic records of what these three men did, and any varieties they may have named have been lost. The first authentic record of named iris seedlings was as recent as 1855. At this time M. Dauvesse, a nurseryman of Orleans, France, offered a half dozen or so new varieties.

Within a dozen years thereafter the growing of iris seedlings was undertaken by many people. The most prominent of these were

Louis Van Houtte and Verdier of France, Krelage, Roozen, and Van Leeuwen of the Netherlands, and Peter Barr of England.

Previous to 1890 it seems that most of the new seedlings were derived from the two species *Iris pallida* Lam. and *I. variegata* L. The results were limited by the potentialities of these two species. Sir Michael Foster about 1880 began collecting iris species and forms from all parts of the world to use in his breeding program. The results of some of his crosses were so striking that other breeders were stimulated, and soon a number of new species combinations began to appear. It is likely that errors of nomenclature may have crept into some of this early work, and there may be some doubt about the alleged parentage of some of the crosses.

Among the modern iris breeders of Europe, the late A. J. Bliss, of England, is probably the best known. He was interested in studying the relationships of many of the present varieties, but he also developed some very fine new ones. He did not specialize in one type of flower but was interested in a wide range of forms.

Figure 18.—Grace Sturtevant, one of the leading iris breeders in the United States. Some of our finest iris varieties owe their origin to her.

The history of iris breeding in the United States dates back to about 1905. At this time Bertrand H. Farr, of Pennsylvania, introduced a collection of superior new varieties from the English firm of Barr. Working with this material, he was able in 1909 to introduce some excellent new seedlings. This work soon stimulated widespread interest, and very shortly large numbers of amateur growers were producing seedlings. In an article of this length it is obviously impossible to mention all the American breeders.

One of the most careful and prolific workers is Grace Sturtevant, of Massachusetts (fig. 18). She has continuously maintained a collection of the very finest varieties to use as parent plants and has developed over 40 new worth-while introductions. Among them

Afterglow, B. Y. Morrison, Queen Caterina, Reverie, and Shekinah are of exceptional merit.

Another American breeder who developed some excellent new varieties was Edward B. Williamson, of Indiana. From about 1910 until his death in 1933 he introduced many new irises. One of the best known came from crossing about 500 flowers of the variety Amas with other varieties. Only one seed pod was formed in these crosses, and one of the seeds in it produced the seedling later named Lent A. Williamson.

J. C. Nicholls, Ithaca, N. Y., is credited with very careful work on iris breeding. He rigidly selects the parents for each cross and keeps a very careful set of records of all his work.

On the Pacific coast, the work of Sidney B. Mitchell and of E. O. Essig is noteworthy. Mitchell has developed many excellent new varieties and recently has devoted most of his time to development of new yellow types. Essig began iris breeding as a hobby and has carried on a series of careful experiments on seed germination under different conditions. He also has introduced several excellent new seedlings. Other American breeders of note are J. M. Shull, of Washington, D. C., and the Sass brothers, of Omaha, Nebr.

The methods employed by some of the better iris breeders are illustrative of the large amount of work necessary to produce really superior types. The late Edward B. Williamson formulated a plan to assure a higher degree of success with his crosses. From his early experiences he knew that many crosses would not produce seed, and the only way to discover which would was to attempt the cross. He decided to use a mixture of pollen in all crosses, reasoning that the prospect of getting some seed would be much better since there was a chance that one or more of the pollens used would be effective. The pollen was gathered from hundreds of flowers and mixed in a receptacle. From 1925 until his death in 1933 he planted each year from 70,000 to 100,000 seeds. He never introduced more than 10 seedlings in any year. The percentage of worth-while varieties is thus rather low.

The methods of J. C. Nicholls are in decided contrast to those of Williamson. Accurate records of both parents are kept. Parents are selected with care, and about 3,000 seeds are planted each year. It is rarely the case that more than 1 iris worthy of varietal status is found in 1,000 seedlings.

Unfortunately little or nothing is known concerning inheritance in iris. Bliss made some preliminary observations on inheritance of leaf pigmentations and coloring of the beard, but the evidence is too meager as yet to warrant a genetic analysis of these characters.

The very early iris breeders simply planted seed and hoped something good would turn up. At the present time the better breeders choose both parents with care and control all crosses. This information about parental stocks, however, has little actual value unless the frequency of superior seedlings arising from each cross is known. Since many of the crosses give only a few seeds or none, a summation of data for the same cross from various breeders would certainly be

worth while. If such information were available a table of breeding qualities of various varieties could be made that would be of some value. Undoubtedly some of the more careful breeders have this sort of information on their own work, but it has not been collected and published.

According to the experience of some iris breeders, one of the serious problems has been sterility. Some varieties are both cross-sterile and self-sterile, others are cross-sterile and self-fertile, others cross-fertile and self-sterile, and still others both cross-fertile and self-fertile. In some cases there are differences of opinion concerning certain varieties, which indicate either an error in nomenclature or that the same variety behaves differently in various localities. In general it can be said that crosses between closely related types have the best prospect of producing seed, with less and less success as the varieties are more distantly related. Likewise, hybrids between closely related types are most likely to be fertile.

Another difficulty is slow and sometimes poor seed germination. To a geneticist attempting to work on the inheritance of some character this is a great obstacle. Whether or not it is due in some cases to poor horticultural practice, it is one of the things that will have to be overcome before much real genetic research can be accomplished.

LILY

To many people in the United States the word lily is closely associated with thoughts of Easter, and they are familiar with only the large-flowered, so-called Easter lily, *Lilium longiflorum* Thunb. This lily is widely grown by florists, who force it for sale as potted plants and also as cut flowers. Easter lilies are rarely grown in outdoor gardens except in very mild climates where they are able to survive the winters and are not exposed to late spring frosts.

One of the best known of the other lilies is the popular so-called Tiger lily, *Lilium tigrinum* Ker. This old-fashioned favorite is a very hardy species and has become widely distributed throughout most parts of the country. Not long after it was introduced from China it escaped from cultivation and is now found growing wild in many sections.

TABLE 2.—*Species of Lilium classified according to date described and continent of origin*

[Compiled from Stoker (*494*)]

When described	Species originating in—			Total	When described	Species originating in—			Total
	North America	Europe	Asia			North America	Europe	Asia	
	Number	*Number*	*Number*			*Number*	*Number*	*Number*	
1753	1	5	¹1	6	1876–1900	5	2	11	18
1754–1800	3	1	3	7	1901–25	4	2	13	19
1801–25	1	1	5	7	1926–36	1	0	5	6
1826–50	0	3	5	8					
1851–75	7	0	6	13	Total	22	14	49	84

¹ Duplicate.

Until very recently only a few lily enthusiasts were familiar with the many beautiful garden forms now available. Most of these new types are wild species from afar that have been introduced by plant explorers. Asia has furnished nearly two-thirds of these, as is shown in table 2. Until quite recently the species introduced by plant explorers more than met demands for new types. The prospect of finding striking and distinct new forms in the wild is now rapidly diminishing, for they do not readily escape the eye of the botanical explorer. Since this is true, it seems that in the future new and superior lilies must come from the plant breeder rather than the explorer.

As recently as 50 years ago only a dozen species of *Lilium* were grown in England, and few sources of bulbs or seeds were available to enthusiasts who wished to grow others. At the turn of the century interest in lilies was waning, but was revived by the introduction of the easily grown *Lilium regale* Wils. from China in 1904. Other new forms from China followed, including *L. sargentiae* Wils. and *L. willmottiae* Wils. The formation of a lily committee by the Royal Horticultural Society and publication of its Lily Yearbook, beginning with 1932, also stimulated interest in England. In the United States the popularity of lilies has kept pace with the growing interest in flowers in general, and the American Horticultural Society has appointed a lily committee this year (1937). New hybrids and more readily available stocks of lily species have also encouraged wider use in gardens everywhere.

A uniform system of naming lilies is essential to an intelligent discussion of lily breeding. Unfortunately for the general public only a few species have well-recognized common names. The use of botanical names is general even in popular accounts, and while these may have a forbidding technical appearance, yet they are in most instances the only generally accepted designations available. For example, the popular Regal lily is known to all botanists and lily enthusiasts as *Lilium regale*. Since most lily breeders become interested in the relationships of the various forms, an outline of the division of the genus *Lilium* into subgenera and sections has been included in the appendix. In this appendix also is a list of lily hybrids, including reports of species crosses from which no named hybrids have been grown. Such a list should be helpful to the amateur hybridizer in pointing out which crosses are readily made and which combinations are difficult or not yet accomplished.

On this continent notable contributions to our array of garden lilies have been made by the late David Griffiths (fig. 19), of the Department, and by Isabella Preston, of the Dominion Experimental Farm at Ottawa, Canada. Griffiths is best known for his work on the propagation of lilies, but he developed and distributed a number of fine Martagon hybrids (*152*), one of which is Star of Oregon. Miss Preston has made great numbers of cross-pollinations with the principal objective of developing hardier lilies for Canadian gardens. Some of her named productions are George C. Creelman, Davmottiae, and the more recent Grace Marshall, Lila McCann, Lilian Cummings, and Phyllis Cox. Many amateurs are active in the United States and in Canada, and some fine hybrids have resulted from their efforts.

In England the Backhouse hybrids produced by Mrs. R. O. Backhouse of narcissus fame are perhaps the best known of the newer lilies, but activity is widespread there as well as on the Continent of Europe.

In the literature of lilies the notation of hybrids has been so casual that Miss Preston felt it desirable to state: "In my notes the seed parent is placed first" (*410*). Other writers have departed from this practice so commonly that it is only by chance reference to one or the other species as seed parent or pollen parent that the reader can tell which cross is discussed. It should also be pointed out that some reported hybrids are based on inferences as to what the parents should have been to produce the observed effects, and, further, that some reported hybrids may be merely asexual offspring of the seed parent. Natural hybrids are not common in *Lilium*, at least in England, according to Grove (*155*); but Preston (*410*) reports two from Canada. *Lilium testaceum* Lindl., *L. elegans* Thunb. (syn. *L. thunbergianum* Schultes), and *L. umbellatum* Hort. are all recognized as hybrids of long standing, in the origin of which man may have played no part.

Figure 19.—The late David Griffiths (1867–1935), who did outstanding breeding work on lilies and narcissus while a member of the United States Department of Agriculture. He is also well known for his work on methods of propagation and production of tulips and hyacinths.

Several examples of supposedly hybrid seedlings that appeared to be identical with the maternal parent were recorded by Parkman (*402*) in 1878. He found that *Lilium superbum* L., emasculated and pollinated by *L. auratum* Lindl., *L. tigrinum* Ker, *L. chalcedonicum* L., or various other species, produced seedlings that were always pure *L. superbum*. When these seedlings were pollinated with other species, the second generation was still unchanged *L. superbum*. Similar results followed the application of pollen of other species to *L. umbellatum* Hort., and the Easter lily, *L. longiflorum*. Griffiths has commented that maternal inheritance is remarkably prevalent in lilies, and (*154*) that *L. regale* yields better results when used as a pollen parent because of this tendency. Stout (*497*) concedes that seedlings of maternal character in *Lilium* may result from wide crosses, without fertilization and production of true seeds. Preston (*409*) has found that seedlings of *L. regale* pollinated with *L. speciosum* Thunb. var. *rubrum* Hort. or with *L. longiflorum* are strictly maternal in character, and that the progeny of a *L. regale* × *longiflorum* cross remained pure *L. regale* in the second generation.

Further reports of similar nature could be cited. Such results might be attributed to late or incomplete emasculation or to ineffective protection against pollen of the maternal species, but such explanations cannot be pressed in the face of reports from careful hybridizers. Some form of parthenogenesis must be assumed in the production of such pseudohybrids, as is suggested by Hall and his coworkers (*191*):

The possibility has to be borne in mind that crossing certain lilies may not result in producing true seed, i. e., by sexual union of the pollen cell with ovule. Excitation due to the foreign pollen may induce the formation from the ovule of a "seed" which is really a bud of the mother plant into which the pollen has not entered.

It has already been mentioned that many hybrid lily types of the past century in particular were noted alike for their beauty and their quick disappearance. Striking examples are Parkman's *Lilium speciosum* × *auratum* (1869) and the reciprocal cross produced by Hovey about 1880, each of which persisted scarcely long enough to be admired and photographed. Most of Burbank's productions are now only memories.

Premature passing of some hybrid types is clearly due to misfortunes of culture before the stock was developed to commercial quantity. It was Griffiths' aim to stress the need for rapid, efficient vegetative propagation to insure establishment of a desirable hybrid as soon as possible, and he devoted much of his energy to improving methods of propagation with this in mind. Some desirable hybrids are inherently slow or difficult to propagate (*151*) and may be lost through the producer's haste to market his creation. Other hybrids, of course, are genetically weak and incapable of long survival, an extreme example of which is the albino seedling.

One of the least excusable reasons for loss of a hybrid is failure to recognize the necessity of vegetative propagation if the stock is to be kept true to type. Very frequently seed of a promising hybrid lily is offered for sale and the seedlings produced are sometimes called by the name of the parent plant. This is obviously a wrong procedure, since it would be very unusual for a first-generation hybrid to breed true. Griffiths (*151*) also calls attention to the fact that there has been a tendency to treat all the hybrids coming from a cross as a variety rather than selecting an outstanding one for vegetative increase as a clonal variety. Such practices have undoubtedly added to the present confusion regarding many named lily hybrids. They are contrary to the fundamental principles of genetics, and lily breeders will do well to discard them.

Another important reason for decline or loss of lily hybrid varieties is the presence of virus diseases such as mosaic (*155*). The viruses are carried in the living cells of the plant and are spread from plant to plant by aphids. When a diseased lily is propagated by division, by stem bulblets, or by scaling, each new plant produced will have the disease. No method is known by which such diseased lilies can be made healthy. If a new hybrid is attacked, it may as well be discarded. Fortunately these diseases are not commonly transmitted through the seed. Accordingly seedling lilies are usually free from virus diseases to begin with and should be grown at a safe distance from affected parent plants and other diseased lilies.

It is generally known that some species of *Lilium* do not readily set seed when pollinated with their own pollen. As early as 1890, Focke demonstrated that *Lilium bulbiferum* L. could be divided into certain groups which would set seed only when pollen was used from a member of another group (*497*). There are many references to the failure of the Madonna lily (*L. candidum* L.) and the Tiger lily (*L. tigrinum*) to develop seeds. Preston states that *L. testaceum* and *L. hansoni* Leichtl., as well as *L. tigrinum*, are self-sterile at Ottawa, Canada. She later (*410, 411*) reports a fertile strain of *L. tigrinum* that she has named "var. diploid." Griffiths cites *L. regale* and *L. longiflorum* as species that set seed only when different plants are interpollinated. Amsler (*4*) reported that *L. brownii* Poit. and *L. parryi* S. Wats. set no seed when selfed, but did when pollinated with other strains of the same species. Stout (*497*) and others who have studied self-incompatibility in *Lilium* made systematic trials with proper attention to emasculation, bagging, and hand pollination, and showed that failure of individual plants to set seed on selfing is widespread in lilies. *L. tigrinum* and its varieties *flore-pleno*, *splendens*, and *fortunei* are triploids (*191*), having 36 chromosomes, and rarely mature functional sex cells. The "variety diploid", however, has the normal diploid number of 24 chromosomes and is self-fertile (*497*). In other species the failure to set seed is not due to inability to develop functional gametes, as is shown by the successful results of interpollinating different lines within a species. Even the triploid *L. tigrinum* will sometimes set seed with the pollen of *L. leichtlini* var. *maximowiczi* (Regel) Baker.

Stout (*497*) mentions occasional instances of failure of lilies to form functional pistils or stamens. He also found poorly formed, nonfunctional pollen in the hybrid *L. testaceum*, which he explained as caused by hybridity and a like condition caused by triploidy in *L. tigrinum*, but he holds that incompatibility is the most important reason for failure to set seed in *Lilium*. In the species *L. henryi* Baker, *L. speciosum* Thunb., *L. superbum*, *L. elegans* Thunb., *L. bulbiferum* subsp. *croceum* (Chaix) Baker, *L. dauricum* Ker, *L. philadelphicum* L., *L. auratum* Lindl., *L. humboldtii* Roezl and Leichtl., *L. kelloggii* Purdy, *L. willmottiae*, *L. roezli* Regel, *L. longiflorum*, he found self-sterility to be the rule but some few individuals set a little seed with their own pollen. Among 59 plants of the common wild lily, *L. canadense* L., 4 fully self-fertile individuals were found, 6 partially self-fertile and 49 wholly self-sterile. Interpollinations of self-sterile plants were successful in nearly all cases. Over 100 plants of *L. hansoni* studied were fully self- and cross-sterile and may represent a single clone. This strain was, however, reciprocally fertile with a new strain of *L. hansoni* received from Manchuria. Stout found no fully self-fertile individuals in *L. candidum*, and cross-fertility was rare and partial until a new stock of unknown source was encountered. Species in which Stout found no self-fertile individuals are *L. hansoni*, *L. candidum*, *L. tigrinum* (excluding the "variety diploid"), *L. parryi*, *L. chalcedonicum* L., *L. brownii*, *L. grayi* S. Wats., *L. sutchuenense* Franch., and *L. maximowiczii* Regel (= *L. leichtlini* var. *maximowiczii*).

Now that the pitfalls of the past are better understood, lily breeding is undoubtedly on a surer basis and prospects are brighter than ever before. The importance of vegetative propagation of hybrids is

becoming recognized, and the methods of vegetative reproduction have been improved. All hybrids start as seedlings and are, therefore, usually free at first from virus diseases, since, as pointed out earlier, these diseases are not commonly seed-borne. This point has become widely appreciated, and efforts are being made to grow as many lilies as possible from seed. When mosaic-free stocks of garden lilies are more generally available, the prospects of increasing a hybrid clone to commercial proportions before it becomes affected will be greatly enhanced.

Some of the possibilities of hybrid combinations may be seen from the tabulation of reported hybrids in the appendix. Crosses are in general more successful within one section of the genus, but a number of successful combinations of Archelirion with Martagon and of Leucolirion with Martagon (see the appendix) are on record. Combinations not yet accomplished may succeed for the persistent breeder. Cytology reveals no discouraging differences in chromosome numbers, except in the case of the triploid *Lilium tigrinum*.

Some of the specific objectives of hybridizers are extension of the flowering season (*155*), extension of the color range in reliable garden forms (*151, 155, 410*), development of garden types even hardier than *Lilium regale* (*410*), and incorporation of superior vigor and adaptability in difficult garden subjects, such as *L. leichtlinii* Hook. f. (*155*), *L. humboldtii* (*153*), and others (*151*). Griffiths suggests *L. henryi* Baker as a promising parent carrying vigor and apparent tolerance to diseases.

Unfortunately, little is known concerning inheritance in lilies. Some of the species that are self-fertile do not give uniform seedlings, which indicates that they themselves are hybrids. This situation is to be expected because of the widespread self-sterility existing in the genus which makes cross-pollination necessary for seed setting.

NASTURTIUM

The native home of the nasturtiums (*Tropaeolum* spp.) seems to be the western coast of South America. They were found there by the early Spanish explorers and introduced by them to Europe from Peru. This probably happened sometime in the latter part of the sixteenth century. The two species that found favor in Spain were *T. minus* L. and *T. majus* L. From Spain they soon spread over most of Europe. In England they were known as "Indian Cresses", the name Indian being used because they came from the Spanish colonies in South America, which at that time were described as the Indies. At first the smaller-flowered *T. minus* was the most widely grown, but on the introduction of varieties of the larger-flowered *T. majus*, the small species was soon neglected. At the present time both types are found growing wild in many sections along the west coast of South America. The two species cross very readily, and many of the so-called Tom Thumb varieties are supposed to have originated in this manner.

The range of colors and color patterns in the modern nasturtium is one of the widest in the flower kingdom. In addition, some varieties are known to bear flowers of various shades on the same plant. The number of varieties listed today is very large, practically all having been developed by professional and amateur efforts.

Not much is known as to the inheritance of flower color. Rasmuson (*427*) has done some work and reports dark yellow as dominant to light yellow, and presence of red to its absence. He also crossed varieties bearing variegated flowers with some nonvariegated flower types. From these crosses he was able to determine that variegation was dominant. In the same investigations it was shown that the dark green color of the leaf was determined by two genes, green being dominant to yellowish green, and both to variegated.

In habit of growth the nasturtium may be divided roughly into three types—the tall or climbing, the bush, and the dwarf bush. When a cross is made between a pure tall and a bush, all the hybrids are tall, and in the next generation there is a ratio of 3 tall to 1 bush. This, of course, shows that climbing is dominant and controlled by a single gene.

Recently considerable interest has been aroused by the introduction of a double form which was named Golden Gleam (fig. 20). The origin of this variety is something of a mystery. It was found about 10 years ago by J. C. Bodger in a flower garden near El Monte, Calif. According to the owner, the seed had been brought into California from Mexico, where it had been introduced from Spain. A search for the type in Mexico, especially in the locality where it was reported, was unsuccessful.

The seed from the California plant was sown the next year and all seedlings proved to be doubles and true also for color. Within a few years the seed was increased to considerable quantities and the new variety introduced. Since other double-flowering plants of the same type were not found, it seems that Golden Gleam probably arose as a mutation from a single-flowered variety. There have been other double nasturtiums, however, one being known as early as 1730, when it was described and figured in colors in the Catalogus Plantarum. The horticultural flore-pleno type mentioned in Bailey's Cyclopedia is probably the same thing. This type, which is still grown to some extent in Europe, differs considerably from Golden Gleam. It is supposed to be entirely double, without production of pollen. Golden Gleam, on the other hand, has anthers and a pistil and sets seed.

Shortly after the discovery of Golden Gleam, cross-pollinations were made to develop other colors. This work was undertaken by Bodger and Burpee. As a result, several mixtures of colors and a scarlet double form appeared on the market a few years ago.

The inheritance of doubleness in nasturtiums has recently been worked out by Eyster and Burpee (*125*). According to these workers, singleness is a simple dominant to doubleness. When a pure single variety is crossed with a double, all the hybrids are single. In the second hybrid generation from such a cross, 78 plants were single and 27 double. This is very nearly a perfect 3:1 ratio. Since it is such a simple situation, we may expect to have all colors represented in the double type in a very few years.

A second double nasturtium has also appeared quite recently. It differs very markedly from both the Golden Gleam type and the earlier double reported from Europe. In the single flower there are five petals while, according to Eyster and Burpee, Golden Gleam varies from an occasional 5-petaled to a 15-petaled flower. The mean petal number
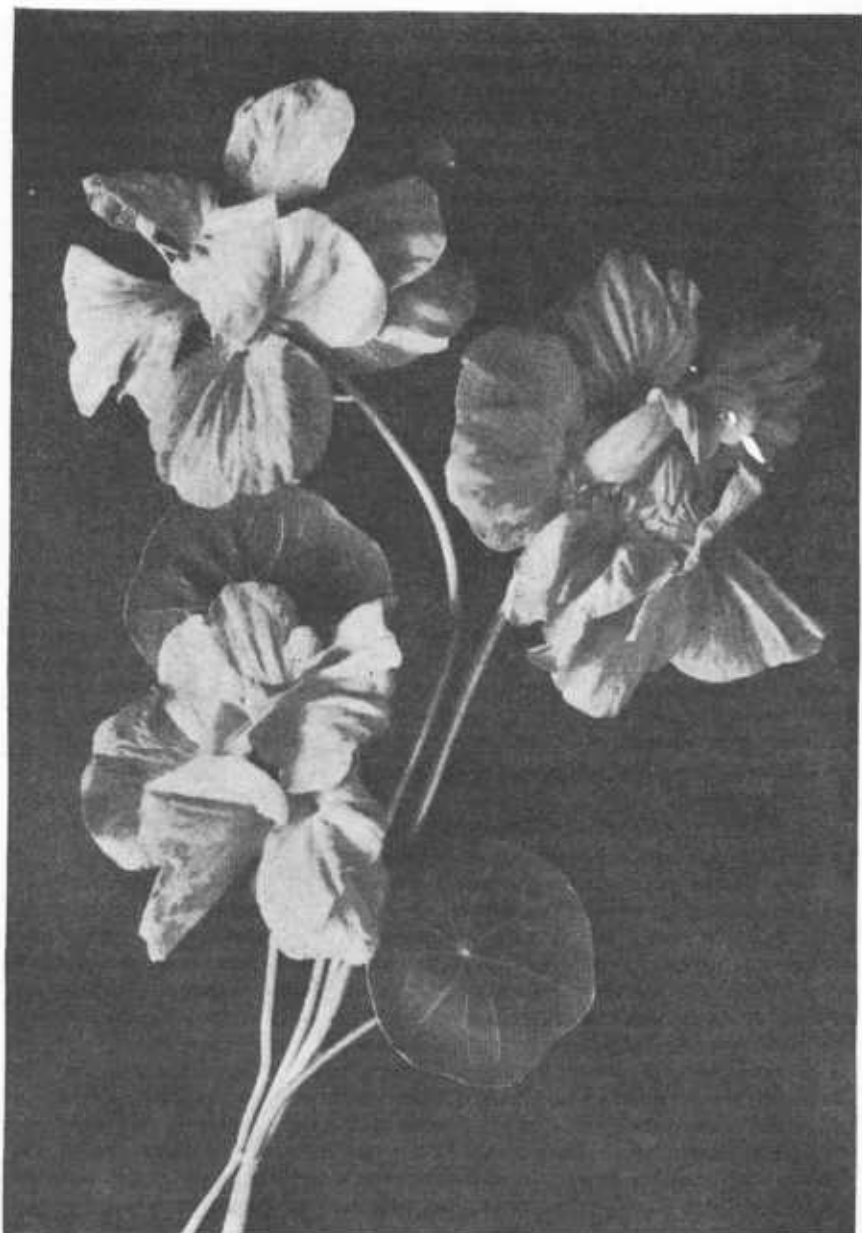
Figure 20.—The double-flowered nasturtium Golden Gleam. This variety was found growing in a garden at El Monte, Calif. It was reputed to have come from Mexico, but a diligent search in that country failed to locate any plants or information regarding it. (Courtesy of Bodger Seeds, Ltd.)

seems to be slightly under 10. The new double type, which is called superdouble, has from 40 to 50 petals, no pistil, and several modified stamens. It does form some good pollen, so it may be regarded as a staminate flower.

The origin of this new extreme double seems to have been spontaneous. It was first noticed in a greenhouse of several thousand double-flowered plants. Since it lacked pistils it could not set seed and had to be propagated by cuttings. The presence of some pollen, however, made it possible to use it as a male parent in crosses with singles and with doubles of the Golden Gleam type. When it was crossed with pure single plants, about half the hybrids were singles and about half superdoubles. Likewise, when crossed with Golden Gleam a 1:1 ratio of doubles and superdoubles was secured. From these results it is apparent that the new superdoubles are all heterozygous (impure) for the new character, which is obviously a simple dominant to both singleness and doubleness. If they had been homozygous (pure), all the hybrids would have been superdoubles in both instances. From this it can be seen that the production of new colors in superdoubles involves an actual hybridizing process. They can be made only by crossing a superdouble with a single or double of some new color. If the gene for superdoubleness is not in the same chromosome as the gene or genes for color, it will be a comparatively simple matter to provide the extreme double in the full color range of the ordinary single nasturtium. If the color gene and the superdouble gene are in the same chromosome the desired result can still be secured, but it will require the growing of a much larger population in order to get the new combination. Unfortunately, adequate linkage data are not available for nasturtiums.

ROSE

The rose is one of the most widely grown and admired of all the flowers. There now exist several thousand named varieties in a wide range of color and form, including types for almost all conceivable conditions of growth. The greenhouse forcing roses, hardy outdoor varieties, climbers, bush, and polyanthas are some of the many types now grown. This wide variation and development has largely occurred in comparatively recent years.

The rose is one of the oldest of our cultivated flowers. It first appears in the early art of long-destroyed civilizations and is frequently mentioned in the Bible and in Greek mythology. It was undoubtedly the favorite flower of many of the rulers of Greece and Rome and was used as a symbol on their banners and shields. This early popularity continued on down through the Middle Ages, and roses were the symbols for the great houses of York and Lancaster in the so-called Wars of the Roses in England.

The genus *Rosa* is a large one with several races, widely distributed, and native mostly in the North Temperate Zone. However, a few species are found near the Equator and even above the Arctic Circle. Many of the finest are native to eastern Asia, but they have not been so highly developed there as in the western part, especially about the eastern end of the Mediterranean Sea.

In Europe during the sixteenth century only a few rose varieties were cultivated and at least half were singles. Two hundred years later there had been only a slight increase in the available varieties. In England at this time there were 21 species in cultivation, and about 30 double varieties. Importations were very rapid after 1789. In this year the Crimson Chinese Monthly, *Rosa chinensis* var. *semperflorens* Koehne, was introduced. Three years later the Macartney, *R. bracteata* Wendl., made its first appearance, and in 1796 *R. rugosa* Thunb. This was followed by *R. multiflora* var. *carnea* Thory, the first rambler rose, in 1804; *R. banksiae* R. Br., in 1807; *R. chinensis* var. *odoratissima* Lindl., the tea-scented rose, in 1809; and the Fairy rose, *R. chinensis* var. *minima* Rehd., and Eduard, a Bourbon type, in 1810. About 1816 a rambler rose, Seven Sisters, *R. multiflora* var. *platyphylla* Thory, appeared. This was followed in 1823 by the microphylla or small-leaved type, *R. roxburghii* Tratt., from China. While only meager records are available, it seems very probable that these new species were used in crosses with some of the native species such as *R. gallica* L., *R. rubiginosa* L., and the so-called Ayrshire roses. By 1829 R. Desportes briefly described 2,562 species or varieties then under cultivation in France. This enormous increase in so short a period is very interesting. It is extremely improbable that it was in any way caused by a sudden tendency to production of sports or mutations. Other factors are more likely to have been responsible, among which importation from other continents and the growing and selection of seedlings were probably two of the most important.

Cultivated roses were probably brought into the United States by the earliest colonists. Very little is known concerning them during these early days, and it was not until after the Revolutionary War that any account is found of the naming of a new variety. This rose, called Mary Washington, may very well be the first truly American production. Shortly following this the Champney or Noisette roses were developed, and soon after, in 1840, Feast Bros., of Baltimore, introduced hardy climbers having our native *Rosa setigera* Michx. as one parent.

At the beginning of this century, most of the rose varieties grown in the United States had originated in Europe. These importations were very frequently disappointing in their behavior, and it was soon realized that varieties should be developed under local environmental conditions. This situation stimulated the efforts of American rose breeders, and today there are hundreds actively engaged in this fascinating work. In an article of this length it is obviously impossible to cover all the contributions of these workers.

One of the earlier pioneers in the breeding of modern roses was the late E. G. Hill, of Richmond, Ind. His first activity with roses began in 1851 when he was employed in the nursery of T. C. Maxwell & Bros. at Geneva, N. Y., where he became familiar with the very best varieties then available. In 1865 the Hill family moved to Richmond, Ind., and in 1881 father and son launched the well-known firm of E. G. Hill. About 1891 Hill began importing the newer hybrid teas to test for cut-flower production under American conditions, and during this last decade of the past century he undertook his own breeding work. It was not until 1904 that two roses resulted which he believed

were superior. These were General MacArthur and Mrs. Theodore Roosevelt. In 1905 Richmond was selected from a large group of red seedlings. These popular varieties were followed by many others.

Another American breeder who introduced many well-known varieties is John Cook, of Baltimore. His first successful hybrid, Souvenir of Wootton, was introduced in 1888. Other well-known varieties developed by him are My Maryland, Radiance, Panama, and Francis Scott Key.

Alexander W. Montgomery, Jr., of Hadley, Mass., is another who has contributed valuable new varieties. Two of his introductions, Hadley and Mrs. Charles Russell, are still very popular. The Dorners, in La Fayette, Ind., have also produced several valuable roses. Probably the best known of these is the widely grown Hoosier Beauty.

The methods used by most of the amateur and professional rose breeders are probably very similar. In general, some ideal type is determined upon and the breeder attempts to secure it by crossing two varieties, each possessing some of the desirable characters. In many instances, the eventual result is far different from the predetermined ideal, in fact, may even surpass it. In general, only a few really successful new roses occur in a population of several thousand seedlings. As an illustration of the odds against securing a really desirable new seedling when varieties are crossed, the following is quoted from an article by Hill (*206*) in the American Rose Annual for 1917:

From the 1914 crosses there were germinated over 2,500 seeds. Each little plant was given special culture, being planted in a bench where it received the same care as that required by the most important forcing varieties. In 1915 the first weeding out of the seedlings occurred, and by 1916 the 2,500 seedlings had been reduced to about 800. These were tested in blocks of five, receiving the most rigid attention and critical scrutiny.

By the opening of 1917, the seedlings have been reduced to some fifteen sorts which Mr. Hill considers worth while going farther with. Of these fifteen several have been selected, named and registered, and propagation is proceeding with the idea of later dissemination.

From this group of 15 came: (1) Columbia, resulting from the cross Ophelia × Mrs. Shawyer; (2) Double Ophelia, from a cross between Ophelia and an unnamed seedling variety; (3) Rose Premier, from a cross between Ophelia and Mrs. Charles Russell; and (4) Mary Hill, from a cross between Ophelia and Sunburst.

Again quoting:

Others of the fifteen sorts are full of promise and will be reported upon later. It may be observed that all of these roses are selected primarily from the forcing or commercial cut-flower standpoint, but it is by no means improbable that several of them may also prove as fine for outdoor use as General MacArthur.

A careful study of these results is very interesting. Suppose all 15 surviving seedlings are finally selected as worth while. The ratio of the total seedlings to the number of good ones is then 2,500:15, or about 1 desirable in 166. It is very probable that the ratio is often considerably greater than this, in some instances reaching odds of over 1,000 to 1.

The very wide variability exhibited by a large group of rose seedlings has been a constant puzzle to many rose breeders. As early as 1889

Lord Penzance, a prominent English rose breeder, published the following statement: "Roses of the first order are, after all, very rare in a sowing of seed, and their production is a veritable lottery, in which chance plays the principal part."

Until fairly recent years, most rose breeders did not even keep a record of parent varieties used in a cross. The lack of this information has been deplored by many observers, but it is doubtful whether such data would have the value apparently attached to it. For instance, the parentage of the widely-grown old favorite, Caroline Testout, is well-known, but it is very doubtful whether any breeder could repeat the cross and secure another Caroline Testout. It is not meant that such a result is impossible, but it is improbable. It might occur if a very large number of hybrid seedlings were grown. There is, however, a possible value in knowing the parentage of rose varieties. It is very probable that we should find certain varieties more apt to produce successful offspring than others. Such information might be helpful in planning cross-pollinations.

The extremely mixed heredity of rose varieties makes planned breeding very difficult. Since propagation is easily accomplished by budding and grafting, this heterozygous condition is not a handicap to the rapid increase of any variety.

TABLE 3.—*Roses developed by Walter Van Fleet*

Year	Variety	Type [1]	Parentage
1895	May Queen	H. W.	*Rosa wichuraiana* × Mrs. de Graw.
1895	Ruby Queen	H. W.	Queen's Scarlet × *R. wichuraiana.*
1895	Clara Barton	H.T.Poly.	Clothilde Soupert × American Beauty.
1895	Alba rubrifolia	H. W.	*R. wichuraiana* × Coquette de Lyon.
1900	Magnafrano	H. T.	Magna Charta × Safrano.
1895	Pearl Queen	H. W.	*R. wichuraiana* × Mrs. de Graw.
1900	New Century	H. R.	*R. rugosa alba* × Clothilde Soupert.
1902	Philadelphia	H. M.	Crimson Rambler × Victor Hugo.
1903	Beauty of Rosemawr	Bour.	
1898	Northern Light	H. W.	
1900	Sir Thomas Lipton	H. R.	*R. rugosa alba* × Clothilde Soupert.
1904	Charles Wagner	H. P.	Jean Liabaud × Victor Hugo.
1902	American Pillar	H. W.	(*R. wichuraiana* × *R. setigera*) × a red hybrid perpetual.
1900	Birdie Blye	H. M.	Helene × Bon Silene.
1905	Rugosa magnifica	H. R.	*R. rugosa* × Ard's Rover.
1907	Garnet Climber	H. W.	*R. wichuraiana* × Lucullus.
1899	Dr. W. Van Fleet	H. W.	(*R. wichuraiana* × Safrano) × Souv. de Pres. Carnot.
1908	Silver Moon	H. W.	(*R. wichuraiana* × Devoniensis) × *R. laevigata.*
1902	Mary Lovett	H. W.	*R. wichuraiana* × Kaiserin Augusta Victoria.
1902	Bess Lovett	H. W.	
1902	Alida Lovett	H. W.	*R. wichuraiana* × Souv. de Pres. Carnot.
1918	Aunt Harriet	H. W.	Appoline × *R. wichuraiana.*
1921	Mary Wallace	H. W.	*R. wichuraiana* × hybrid tea.
1923	Heart of Gold	H. W.	(*R. wichuraiana* × *R. setigera*) × *R. moyesi.*
1925	Sarah Van Fleet	H. R.	*R. rugosa* × a hybrid tea, possibly My Maryland.
1925	Dr. E. M. Mills	H. R.	
1926	Breeze Hill	H. W.	*R. wichuraiana* × Beaute de Lyon.
1926	Glenn Dale	H. W.	*R. wichuraiana* × Isabella Sprunt.
1927	Ruskin	H. R.	*R. rugosa,* Souv. de Pierre Leperdrieux × Victor Hugo.

[1] Abbreviations have been used to designate the class to which the rose belongs:

H. W.=Hybrid wichuraiana.
H. R.=Hybrid rugosa.
H. T.=Hybrid tea.
H. T.Poly=Baby rambler with hybrid tea characteristics.
H. M.=Hybrid multiflora.
H. P.=Hybrid perpetual.
Bour.=Bourbon.

While American rose breeders were not at first so active as Europeans in producing hybrid teas, they have accomplished much in developing hardy outdoor roses. One of the leaders in this work was

the late W. Van Fleet (fig. 21), who continued his rose-breeding activities after he became a member of the Department of Agriculture. He was an industrious worker, making many thousands of crosses and keeping accurate records of his work. His objective was to produce continuous blooming roses for common dooryard culture under the diverse climatic conditions of this country. In order to develop such types he utilized all available vigorous species of pleasing aspect, as well as strong-growing garden forms, crossing them with highly developed florists' varieties. In this manner he hoped to secure plants that would combine the really desirable characters of the parents. Two varieties developed by him were introduced posthumously.

The complete list of Dr. Van Fleet's varieties is given in table 3, where they are arranged in the order of their introduction. It is interesting to note how few species entered into the formation of these varieties. Thirteen of the nineteen had *Rosa wichuraiana* Crépin as one parent; three had *R. rugosa*, two *R. setigera*, one *R. multiflora* Thunb., and one *R. moyesi* Hemsl. and Wilson. Some of these introductions have gained widespread recognition and are widely grown.

Figure 21.—The late Walter Van Fleet (1857–1922), of the United States Department of Agriculture, who did outstanding work on breeding hardy outdoor roses. He set as his goal the development of hardy dooryard roses that would bloom continuously from early spring until frost.

Another breeder of hardy roses is N. E. Hansen, of the South Dakota Agricultural Experiment Station at Brookings. He has been working for some time to develop roses to withstand the severe winters of that section. His first introduction was the variety Tetonkaha, which appeared in 1912. In 1926 a second variety, Tegala, was released, and in 1927, 13 others were introduced. All these varieties have proved hardy at the Brookings station and have been distributed in the Northwest prairie region.

The great diversity of form and habit in any group of rose hybrids is easily understood. To the geneticist it is the naturally expected outcome when two highly heterozygous plants are cross-pollinated. While the records of early hybridization in roses are none too authentic, they do at least show that the ancestry of our modern varieties is very complex. Thus the hybrid teas probably originated from a cross between a hybrid perpetual and a tea rose. The teas are supposed to have come from *Rosa odorata* Sweet. The hybrid perpetuals have a very complex ancestry. As far as can be determined, the earliest progenitor was a damask rose called The Four Seasons.

It was being grown commercially in 1790 and was probably crossed extensively with the French and Provence roses to give rise to the damask perpetual. It seems that these were then crossed with China roses, from which came the hybrid China types. According to the records of this period all roses in this last group were apparently sterile, but in 1830 a M. Guerin produced a hybrid named Malton, which proved to be fertile. A second fertile hybrid called Athalin was produced the same year by Jacques, gardener to the King, at Neuilly. It is very likely the damask parent of each was a descendant from the variety The Four Seasons. A few years later the variety Athalin was crossed with Rose du Roi, a damask perpetual. Some of these crosses were called hybrid damasks and were the direct forerunners of the hybrid perpetuals. In 1837, M. Laffay, a florist located at Bellevue, near Paris, introduced Prince Albert and Princess Helene, two new varieties. They were of the hybrid-perpetual type, and M. Laffay is usually credited as the originator of this group. He later produced other varieties, among which was La Reine. In 1844, groups of hybrid Chinas, bourbon perpetuals, hybrid damask perpetuals, hybrid Gallicas, and moss roses were all combined to form the hybrid perpetual group.

The hybrid teas, then, have a very diverse ancestry. This complexity has been greatly multiplied by crosses among themselves, so that our modern hybrid-tea varieties are undoubtedly a conglomeration of many ancestral characters. Is it any wonder that even in a group of thousands of hybrids from seed, no two are exactly alike?

The sudden spontaneous appearance of so-called sports in roses is a well-known phenomenon. The frequency with which they appear is not known, although some varieties are supposed to produce more than others. This, however, is probably based on the limited numbers considered worthy of introduction rather than on the total actually produced. There is little information about such sudden changes in parts of the plant other than flowers. In many instances the sport involves only a slight change in flower color, although very sharp breaks, such as from red to white, are also known.

These mutations in the hereditary material in the cells may occur at different stages of development and in different parts of the plant. When, for instance, a red rose produces a branch bearing white flowers, doubtless a change has occurred in the petal cells that carry the color pigments. The change may have occurred in the bud that produced the side branch, or it may have occurred at any time during the growth of the shoot and flower bud. Sometimes the change in hereditary material comes after the flower bud is almost fully developed. In such instances we may have bicolored flowers, each pigment being restricted to a very definite sector.

It may sometimes happen that a particular bud taken from a mutated branch fails to produce the new flower type. Such a situation is called a reversion by rose breeders, but it probably indicates that the mutation occurred after this bud had been formed.

No one as yet has been able to induce a sport in roses or explain the forces that bring about the change under natural conditions. Some of the future research on roses will undoubtedly be concerned with such matters. It is possible that exposure of buds to X-rays, radium,

heat, or some chemical might induce radical changes. Until such time one must depend on the chance occurrence of mutations. Unfortunately the erroneous idea has become current that special credit is due the introducer of a new rose sport. Actually the rose breeder has no control whatever over its appearance. He is simply fortunate in having the mutation occur in one of his plants. Such introductions should not be classed with actual breeding work where planned cross-pollinations are made and thousands of seedlings grown. Even in the latter case, our present methods are very little advanced over what they were 45 years ago, when Lord Penzance called rose breeding a lottery.

The contributions of science to rose breeding have been concerned chiefly with pollen studies, studies of the chromosomes of the various species, and methods of hastening seed germination. The classification of the genus *Rosa* into species has been a very difficult problem. Various workers have from time to time revised the classification, and there has not been any general agreement among them. This confusion is probably caused by the lack of agreement on what constitutes a species, as well as by the undoubted heterogeneous nature of roses. In early days, as well as now, natural crosses between wild roses probably occurred, giving rise to new intermediate forms. When rose growing became so popular, amateurs began making cross-pollinations between all available types, thus further complicating the situation.

At the present time most rose varieties and so-called species are actually mixtures of many types. Classification as botanical species is practically impossible. Undoubtedly many of our present so-called species are simply hybrids, as is indicated by the degrees of partial sterility found.

An interesting study of the pollen of several wild species and some species hybrids was made by Erlanson (*120*). Her method consisted in staining the pollen and counting the percentage of poor, shriveled grains. She found that poor pollen exists in all our native American rose species. It averaged about 20 percent infertile in all except *Rosa acicularis* Lindl. and *R. palustris* Marsh., where it was about 10 percent. Even relatively fertile individual plants had as much as 25 percent infertile pollen. In hybrids the percentage of poor pollen was usually very much greater than in the wild species, and the conclusion was reached that any wild rose plant with over 70 percent of infertile pollen and setting little or no fruit was probably a first-generation hybrid.

Observations of the chromosomes of roses have also thrown some light on the species problem. Rose species have been found with 14, 21, 28, 35, 42, 49, and 56 chromosomes in the body cells. These numbers increase each time by 7 and are called a polyploid series. According to Hurst there are distinctly different seven-chromosome groups. He assumes at least five such groups, which he designates as A, B, C, D, E. Different combinations of these five chromosome sets would certainly explain much of the wide variability in the genus.

One of the greatest handicaps faced by rose breeders is the matter of irregular seed germination. Seed from some species sprouts readily, while that from others may not start growth for several years. In

1926 William Crocker, of the Boyce Thompson Institute at Yonkers, N. Y., published results of his studies on after-ripening and germination of rose seeds. The seeds were stored at various temperatures in moist granulated peat. The best temperature for both species and hybrids was found to be 41° F. In some cases the acid in the peat injured the rootlets of some roses, but this can be remedied by neutralizing the peat with a little lime or by using nonacid peat if it is obtainable.

The future of rose breeding depends to a considerable extent on the accumulation of fundamental information on inheritance of rose characters, and on breaking away from many of the established practices. As stated earlier, the accumulation of parentage records is of little value unless it is accompanied by information on numbers of seedlings grown. Undoubtedly some parents will give better progenies than others. This information for some varieties is probably known by some breeders but is not generally distributed. It also seems advisable to start self-pollinations of many present varieties, since they are already so heterozygous that they will probably give rise to something of value. Above all there is a need for systematic investigation by trained workers at institutions well equipped for genetic and breeding work with roses. Such a program would undoubtedly clear up much of the present confusion.

Snapdragon

The early history of the cultivated snapdragon (*Antirrhinum majus* L.) is not known. Some records indicate that it was first grown in Italy, whence it spread to the remainder of Europe. At the present time the species is found growing wild in many spots along the Mediterranean coast west of Italy. In one of the earliest published accounts, in 1578, there were described several color variations and two distinctive leaf types, the narrow and the broad. A little later, five varieties, white, purple, blush, yellow, and variable, were known. Soon after this a double-flowered form and one with variegated leaves appeared. At the beginning of the nineteenth century several striped and spotted varieties were listed by various growers. By 1824 a wide range of colors existed from rich orange and yellow to white, with the same types in reds and purples as well as many bicolor forms.

The first-named botanical varieties of *Antirrhinum majus* did not appear until about 1830 or 1835. Among these were *reticulatum*, *youngii*, and *carophylloides*. In 1844 a deep blood-red double-flowered type appeared. The earlier doubles had ranged from white to rose. In the next few decades countless horticultural varieties were introduced each year and were sold as high as $1 per plant. At this time propagation was entirely by cuttings. In 1850, George Parsons, of Brighton, England, introduced a variety that was a distinct change in the arrangement of the colors of the flower. It was white with a deep rose band in the form of an edging to the petals. It was distributed by E. C. Henderson & Sons, in 1852, under the name of Hendersonii.

The snapdragon did not come into its own until the latter half of the nineteenth century. All the earlier varieties had been propagated only by cuttings, and very little had been done with seedlings. The

climate of Scotland and England was very favorable for the production of snapdragons of fine quality, and the flower soon became very popular. The demand for newer and improved varieties stimulated the growing of seedlings, and hundreds of new types were soon developed.

At the present time snapdragons are roughly divided into two groups—(1) florists' varieties and (2) types for outdoor culture. Some varieties, of course, may be placed in both groups. In England and Europe generally, the chief interest is in the outdoor sorts, while in the United States the forcing or greenhouse types are the most important.

The snapdragon flower is so constructed that smaller insects find it very difficult to gain entrance to the nectaries. It requires considerable effort even on the part of a large bumblebee to open the two parts of the corolla. The flower is, nevertheless, frequently visited by large bees, and undoubtedly considerable cross-pollination occurs. Because of this situation, varieties of snapdragons grown for seed should be separated a considerable distance from others. This is especially important for florist varieties, where it is essential that strains be true for type and color.

The practice of growing snapdragons from seed did not become very general until early in the present century. In England and France, seed had been offered by various seedsmen for some time. Most of the old standard varieties, however, were still increased solely by cuttings. In this country, nearly all florists propagated entirely in this manner. As a result many local varieties arose but were not widely distributed. In 1913, snapdragon rust suddenly appeared in the vicinity of Chicago. It had been known in California and along the Pacific coast since 1896. Within a few years after its appearance the disease spread to all sections of this country, to Mexico, and to Canada. The result was almost disastrous to greenhouse snapdragons and practically eliminated propagation by cuttings. The moist conditions and warmth in the cutting bench were also the optimum conditions for snapdragon rust. This situation, and the fact that the disease was not seed borne, stimulated development of better seed-propagated strains. Within a short time a great number had appeared, and today the total list includes many hundreds of varieties.

Most of the present-day varieties have probably arisen from chance crosses made when the commercial seed crop was produced. Even though the seedsman rigidly removes all off-colors and types, the seed produced will usually contain some crosses made by bees. The florist or grower then finds offtype plants the next year. In addition to this source of contamination it is also very probable that some strains usually contain a few hybrids, which carry recessive characters that do not show up until the next year.

Following the widespread distribution of rust, the popularity of the snapdragon began to wane in this country. The florists were able to control the disease under glass, to some extent, by careful attention to watering and maintaining a temperature unfavorable to its development. Plantings outdoors, however, continued to suffer, and the snapdragon began slowly to disappear from parks and home gardens. In California the growing of snapdragon seed was a rather precarious

undertaking. In some years a fair crop might be secured, but on the average the yields were very poor. Many attempts to control the disease by spraying were on the whole unsuccessful.

In 1922 E. B. Mains, then at Purdue University, found two snapdragon plants that showed some resistance to rust. In 1927 he distributed seed to several investigators. Continued selections and self-pollinations in descendants of these strains finally resulted in the development of highly resistant strains of snapdragons. The inheritance of this resistance has been studied by Emsweller and Jones (*117*), White (*545*), and Mains (*327*). In all cases resistance was due to a dominant gene. The inheritance of resistance is shown in figure 22. At the upper left are shown a flower and leaf of a susceptible variety; in the upper right a flower and leaf of a resistant plant; directly between and below, a flower and leaf from the hybrid resulting from a cross between susceptible and resistant. Since resistance is dominant, the first-generation hybrid is completely free from rust. At the bottom are shown flowers and leaves from four of the second-generation plants. Three are resistant and one is susceptible. This count of 3 to 1 is the typical Mendelian ratio when a single pair of contrasting genes is involved. The actual figures from such a cross made in California were as follows: All of the 562 first-generation hybrid plants were completely resistant. One of them was self-pollinated and 550 second-generation plants were grown from the seed. In this large population 405 plants were resistant and 145 were susceptible. A perfect 3:1 ratio would have been 413 resistant to 137 susceptible. The ratio actually secured was off just eight plants. Such a small deviation is not significant, and the ratio secured undoubtedly represents what is called a simple monogenic segregation. Resistance was also found in other *Antirrhinum* species imported from western Europe by the Division of Plant Exploration and Introduction, but these were not used in the breeding of the rust-resistant strains mentioned.

Recently in several localities in California, some of the supposedly resistant plants have again succumbed to rust. Such a situation is not unusual, being common in grain varieties bred for resistance to certain strains of the cereal rusts. It is possible that the condition in California is caused by a new strain or physiological form of the rust organism. Since the rust parasite on the snapdragon is itself a small plant, it is not unusual that it should produce a new strain able to attack otherwise resistant plants. If this should prove to be the situation, the production of rust-resistant strains of snapdragons will be more difficult in those sections where more than one physiological race of rust occurs.

The genetics of the snapdragon has been extensively studied by a large number of workers. The inheritance of color is very complex. According to Miss Wheldale, magenta is in general the most dominant color and yellow the most recessive. By this is meant that magenta is dominant to practically all other colors, while yellow is usually recessive to all others. This explains why seedsmen find that yellow varieties and strains are usually very easy to purify. Since yellow is recessive, plants can exhibit this color only when pure for it. In the same investigations, crimson was dominant to bronze, bronze to

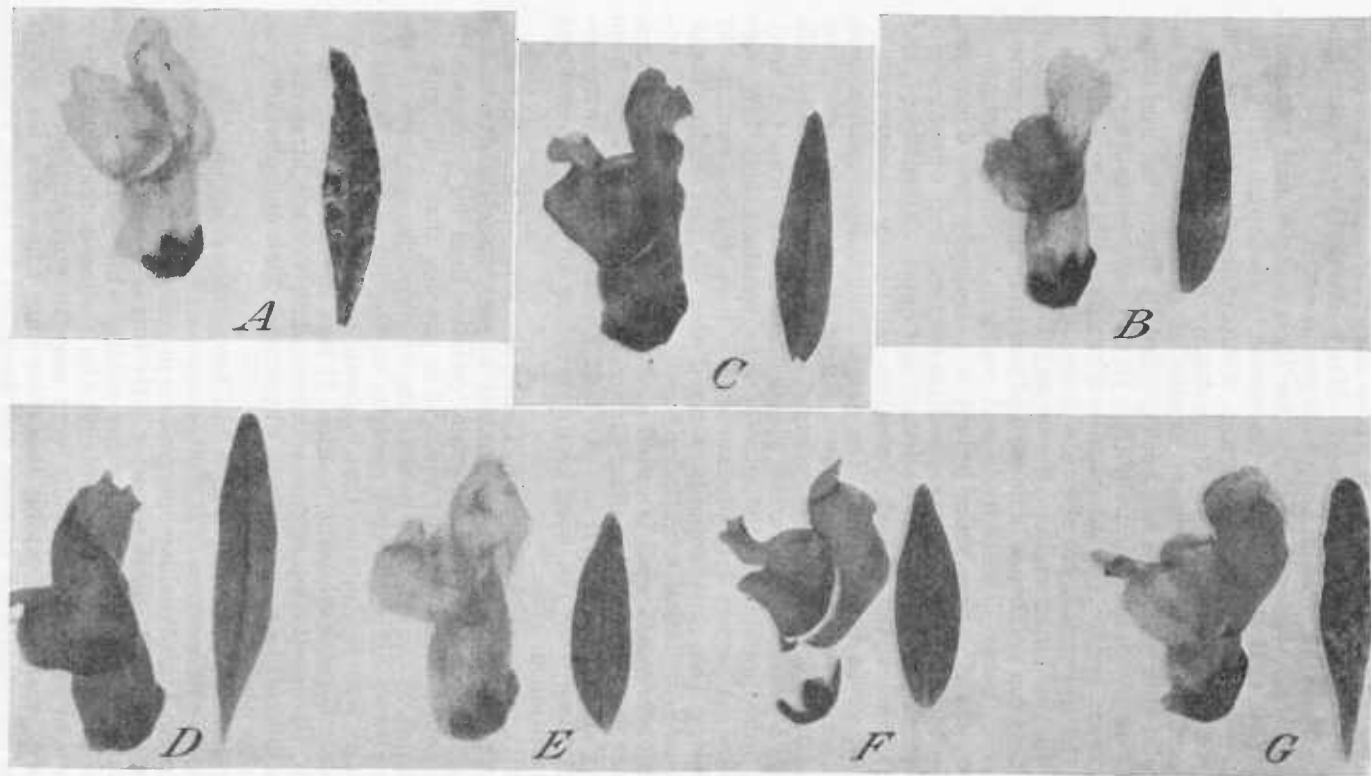Figure 22.—The way in which rust resistance is inherited in the snapdragon: *A*, Flower and leaf of the susceptible variety; *B*, those of a resistant plant; *C*, resistant hybrid resulting from cross-pollination of *A* and *B*; *D*, *E*, *F*, *G*, flower and leaf from each of four plants descended from the resistant hybrid *C*; this second hybrid generation had a ratio of 3 resistant plants to 1 susceptible.

yellow-tinged bronze, magenta to rose doreé, and rose doreé to ivory-tinged rose doreé. Delilah forms, in which corolla lips are colored and tube is colorless, were recessive to the corresponding nondelilah. For example, crimson was dominant to crimson delilah.

STOCK, DOUBLE-FLOWERED

The early history of the stock (*Matthiola incana* (L.) R. Br.) is very obscure. The first authentic records indicate that it was known to the Greeks and Romans and prized by them chiefly as a medicinal herb. By 1542 at least three colors, purple, red, and white, were known, but only in single-flowered types.

The first mention of a double form was in 1568, when a Belgian botanist, Dodvens, described it in a paper dealing with sweet-smelling flowers suitable for chaplets or garlands; and in 1581 an actual illustration appeared. At this time the flower was described as being so double that it was completely sterile. It is not known just when the double form appeared, but it was probably a mutation from the single. From the scant records of the period it seems that the only method of reproducing it was by cuttings. It was not until 1629 that any statement appeared indicating that double-flowered plants could be obtained from seed of singles.

Unfortunately, one of the earliest descriptions of double-flowered stock stated that the doubling was the result of special treatment and frequent transplantation. This belief was held for a long time and many special practices based on superstition developed in the culture of stocks. One of the most interesting descriptions of such practices appeared in a book on gardening in 1675:

Single Flowers Doubled

Remove a plant of stock when it is a little woodded and not too greene, and water it presently; doe this three days after the full, and remove it twice more before the change. Doe this in barren ground, and likewise three days after the new full Moon remove againe, and then remove once more before the change. Then at the third full Moon, viz., eight days after, remove againe, and set it in very rich ground, and this will make it bring forth a double flower; but if your stocks once spindle, then you may not remove them. Also, you must shade your plant with boughs for three or foure dayes after the first removing; and so of Pinks, Roses, Daysies, Featherview, etc., that grow single with long standing. Make Tulipees double in this manner. Some think by cutting them at every full Moone before they beare to make them at length to beare double.

As mentioned earlier, the double-flowered stock plants were propagated by cuttings, but how they came from seed of the singles remained a mystery until it was cleared up by the genetic and cytological research of Saunders (*463*), Frost (*135*), and Philp and Huskins (*408*). For a long time it was generally believed that the double-flowers produced some pollen, which fertilized the singles and formed seed that produced doubles. Directions are still occasionally given for selection of seed from single-flowered plants surrounded by doubled-flowered. An examination of the double flowers, however, discloses no pollen whatever, and it seems certain that if any is ever produced, it is only on exceedingly rare plants.

The differences between a single and a double flower are very striking. The single has four petals, four stamens, and a pistil. When fertilized it produces a long, narrow, flattened fruit containing

from 30 to 60 seeds. The double flower is composed entirely of petals, which vary from 40 to 70 per flower. There is no trace of stamens or pistil, and, of course, no seed is formed.

The double-flowered plants are desired by both florists and gardeners, and because of this there is active competition among growers of stock seed to produce high double-throwing strains. Accurate counts made by seedsmen have revealed many strains with 80-percent and a few with as high as 90-percent doubles. Usually, however, the proportion secured by florists and home growers is far less. The seedsmen themselves encounter sharp fluctuations; a strain producing as high as 80-percent doubles one year may drop to 50-percent or less the next. As a result of this apparent instability, seedsmen, florists, and gardeners have entertained a belief that doubleness must be controlled by some external environmental factor or factors.

Modern genetic research has now found the fairly simple explanation of this situation. It also points the way to production of reasonably nonfluctuating, double-throwing strains that produce the maximum percentage of doubles. When a large number of single plants are self-pollinated and all seedlings of each one saved, it has been discovered that the singles are of three sorts. Type 1 produces only single-flowered plants, type 2 produces 3 single-flowered plants to 1 double-flowered, and type 3 produces about 54 percent of double-flowered plants and 46 percent of single-flowered. The single-flowered progeny of type-1 singles never produce any doubles in their selfed progenies; they are pure for singleness. The single-flowered progeny of type-2 singles are of two kinds, one-third being pure for singleness and two-thirds like type 2, that is, producing progenies with 3 singles to 1 double. Most of the single-flowered progeny of type-3 singles repeat the performance of their parents, each again producing about 54-percent doubles.[8]

It is now easy to understand how fluctuations in percentage of doubles may occur from generation to generation. Even though a seedsman practices careful plant selection and saves seed only from the high-double strains, he cannot predict with accuracy the ratio of doubles to singles from year to year. It seems highly probable that nearly all stock seed is a mixture of all three types of singles. The percentage of doubles that will develop in any strain, then, is influenced by the number of pure and heterozygous singles that were in the seed field. Since at present there is no certain method of distinguishing the three types of singles except by a progeny test it seems that with ordinary methods of seed production the number of doubles will continue to fluctuate from generation to generation.

The preceding explanation accounts for yearly changes in the proportion of doubles, but it does not explain the occurrence of strains with more than 54 to 57 percent. In fact, it sets such an amount as the maximum proportion that can be secured. How can the strains with over 80 percent of doubles be explained? Miss Saunders has given the explanation. About 20 years ago she noticed for several years the high percentage of doubles developing in a bed of stocks. It occurred to her that some sort of artificial selection could account

[8] It has been shown that occasional pure single plants appear even in type 3. They, of course, bring down the percentage of doubles expected from this type and are an additional source of confusion.

for it.   A few years later she planted 8 to 10 seeds in each of a large number of pots.   When the seedlings were well established, those in each pot were numbered according to their size.   When the plants finally bloomed, it was found that most of the large ones were doubles and the small ones singles.   In 1923 White (*546*) at the Maryland Agricultural Experiment Station conducted a very similar experiment. He grew a large number of seedlings and then graded them into groups on the basis of size.   When the plants bloomed, he too found that most of the large ones were doubles.

. S. L. Emsweller has also investigated the problem in genetic studies with stocks.   The seedlings were not graded by size, but as soon as the first true leaves were developed, about 150 plants from each of several varieties were transplanted into small pots.   All seedlings of a progeny were saved.   When the small plants were established, the height, spread, and stem diameter of each were measured each week until the plants began to bloom.   They were then classified as doubles and singles, and the mean height, spread, and stem diameter for each group were computed for the weekly intervals.   In all cases it was very clear that the double plants were more vigorous than the singles, even in the seedling stage.   This does not mean that the smallest double plant was larger than the largest single; there were always a few plants of each type that overlapped.   It was possible, however, by selecting only the very largest seedlings, to secure 85 to 90 percent of doubles (fig. 23).

Thus the occurrence of unusually high double strains is readily explained.   If anyone, florist or gardener, has more seedlings of stocks than are needed, he will invariably discard the weak, small ones and save the largest.   On the California flower-seed ranches, stock seed is sown in rows in the field.   When the seedlings have become well established they are thinned by hand, and naturally the stronger plants are left.   This readily explains the frequent occurrence of rows with 80 to 85 percent of doubles.   Such rows, of course, came from parent plants that gave the highest possible percentage of doubles.

In the light of these facts, certain recommendations for growing seed of stocks can be made.   In the absence of definite information on natural crossing in stocks, it is advisable to self-pollinate all plants selected.   A small sample of seed from each selfed plant should be sown in a separate row.   Random samples of these seedlings, the first 50 in each row, should be transplanted, the lots again being kept separate.   These trial plantings will indicate the genetic type of the parent of each row.   Seed from pure singles will give only single-flowered plants; that from simple hybrids, about 3 singles to 1 double; and that from the so-called ever-sporting type, slightly more than 50 percent of doubles.   The seed of all pure singles and simple hybrids can then be discarded and a seed crop grown from plants that produced the maximum number of doubles.   Such a procedure would require 2 to 3 years but would certainly give high-quality seed.   In many sections of California it is possible to maintain such a planting for several years. Emsweller has done so and secured a greatly increased seed yield the second year.   It is recognized, of course, that this method would involve extra expense, but it has been profitable with delphinium, hollyhock, and columbine, and it should be with stocks also.   If seed

of this type were generally available, and florists and gardeners rigidly discarded all weak seedlings, they should have little trouble in securing stocks running close to 90 percent double. This means that over twice the ordinary amount of seed should be planted, since slightly more than half the seedlings would be discarded in thinning out on the basis of size.

There are several types of stock plants (fig. 24) varying in habit of growth, earliness, and flower color. Unfortunately the importance of
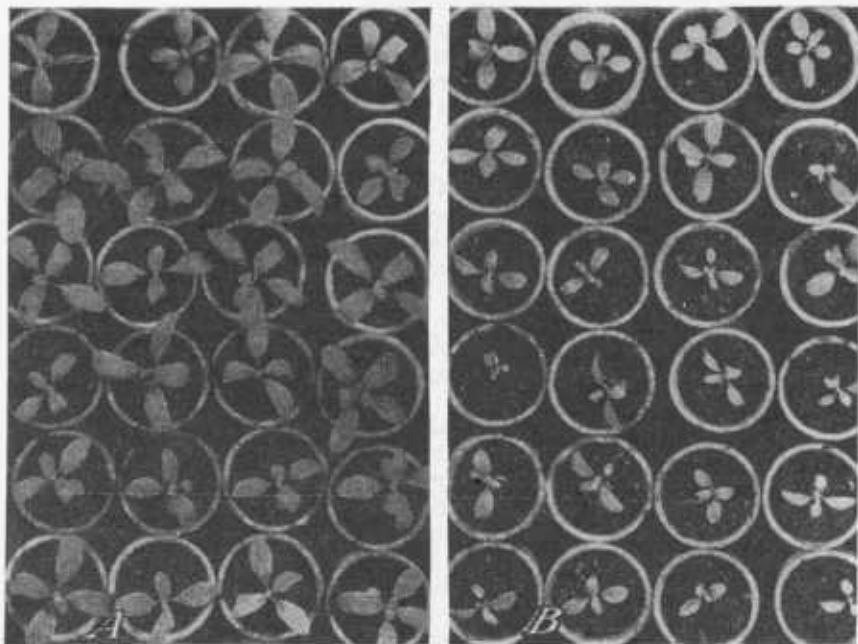

Figure 23.—Stock seedlings selected for size after transplanting: *A*, Group of the extremely large plants, 90 percent of which were double-flowered; *B*, smallest plants, 18 percent of which were double-flowered.

the problem of double flowers has retarded work on inheritance of these characters. Some data are available, however, on inheritance of tall versus dwarf plants and branching versus nonbranching. Tall is dominant to dwarf, and in the second hybrid generation there will be found three tall plants to one dwarf. The situation is not so clear-cut for branching crossed with nonbranching. The first-generation hybrid is branched, and in the second generation there is a close approach to a ratio of 3 branching to 1 nonbranching. These non-branching plants, however, have some tendency toward branching, which the original nonbranching parent plant did not have.

The future breeding work with stocks will probably be concerned with the inheritance of other important characters. There is also need for the discovery of some simple seedling characteristic to enable florists and gardeners to select with certainty double-flowered plants in the seedling stage.
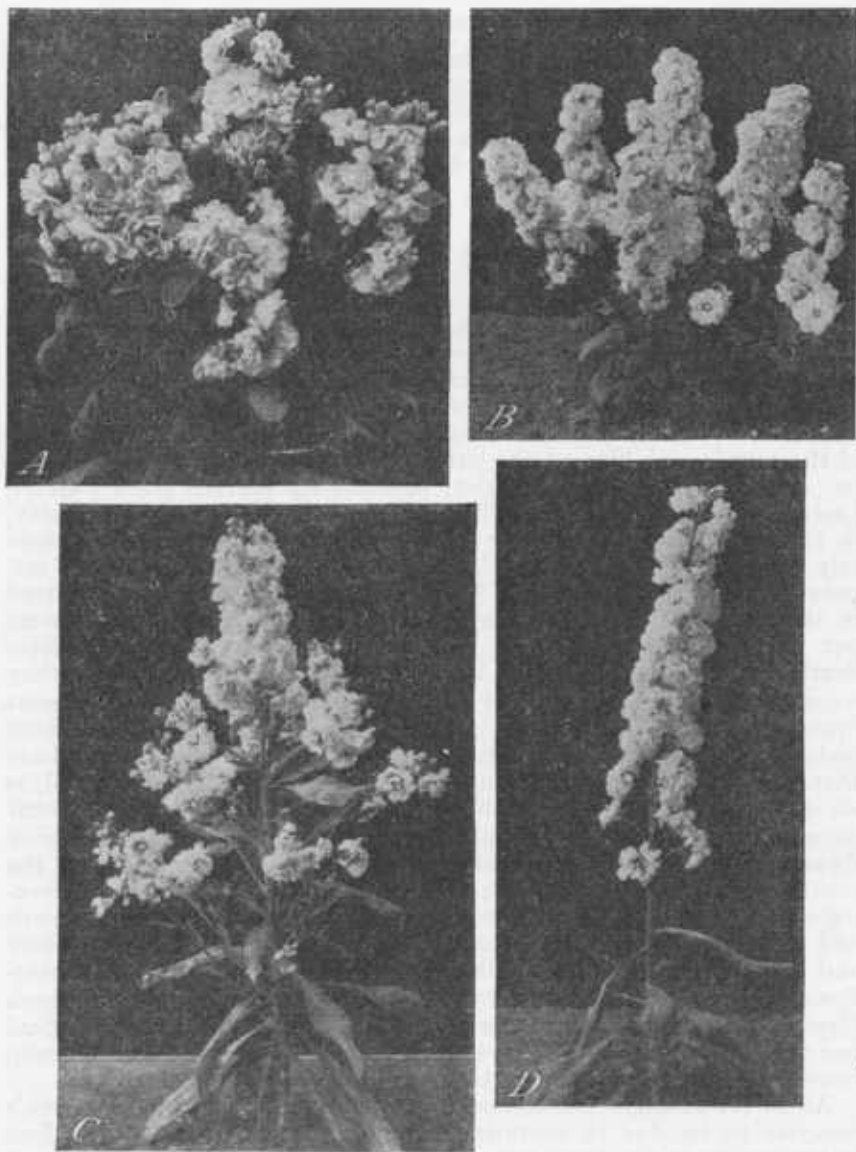
Figure 24.—Four types of double-flowering stock showing variation in growth habit. There are many varieties of each kind including a wide range of colors. (*A*) The tall ten weeks and (*B*) the dwarf ten weeks types are used mostly for bedding, are very early bloomers, and are easy to grow. (*C*) The imperial (branching) and (*D*) the column (nonbranching) types are grown mostly under glass by florists. The column sorts (*D*) are valued for their tall single spike and for adaptability for close planting, thus yielding more salable flower spikes per square foot of greenhouse bench.

SWEET PEA

The sweet pea (*Lathyrus odoratus* L.) was introduced into the Netherlands and England from its native Sicily in 1699. From a figure and description published in 1700 the original type is recognizable as a tall plant reaching a height of 6 or 7 feet, with short flower stems bearing two blooms each. The individual bloom was small and fragrant. The standard was erect, narrowed at the base and cleft at the top. In color the standard was reddish purple, the wings light bluish purple. Figure 25 shows a type closely resembling the wild *Lathyrus odoratus* in comparison with a modern flower.

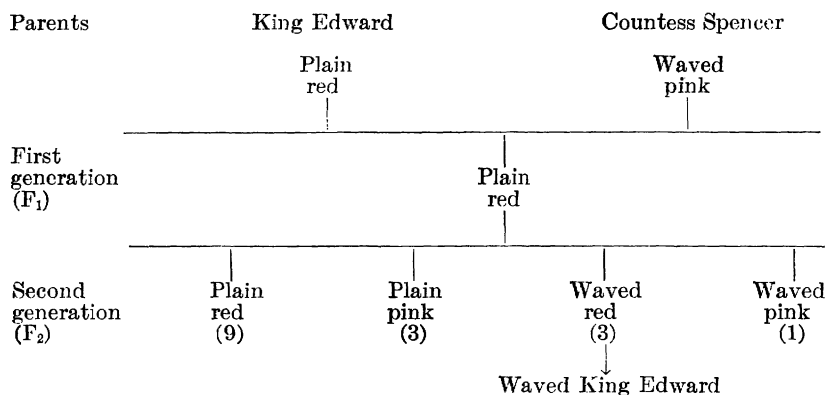The evolution of 500 or more distinct garden varieties from this unassuming beginning has been admirably traced by Beal (*40*), and the significance of mutation and hybridization in the process has been interpreted by Babcock and Clausen (*8*). White forms appeared in 1718. In 1731 Painted Lady—pink and white in place of the purple and blue of the original type—was introduced. Scarlet, a brighter self-colored variety presumably derived from Painted Lady, appeared in 1793. Then followed in 1806 a blue variety, in 1817 a striped type, and in 1824 the so-called yellow, more properly primrose. New Large Purple, listed in 1845, implies an improvement in size of bloom. Marked increase in size also occurred in the Countess Spencer variety (1904). The original two flowers per stalk were increased to three with the advent of Invincible Scarlet in 1865 and Crown Princess of Persia in 1868, and they were further increased to four blooms per stalk in the more recent Spencer type. The form of standard was differentiated into three distinct types: grandiflora, erect but larger and broader at the base than the original, appeared in 1888; hooded, with edges inrolled, is an early type; Spencer, with waved standard, is a more recent development. Changes in habit of growth include two recessive dwarf types, the cupid (prostrate) and the bush (erect), and the commercially important winter-flowering type. The winter-flowering sorts are distinguished from other sweet peas by prompt growth and flowering under winter forcing conditions and by lower stature and shorter flower stems. Blanche Ferry, the first of the winter-flowering types, was selected by the wife of a quarryman in northern New York for 25 years before it reached the trade in 1889. Beal has traced the subsequent development of the winter-flowering group from this and subsequent mutations.

All of the changes mentioned thus far are considered in Babcock's analysis to be due to mutation from the original type. The first hybridization in the sweet pea was undertaken about 1880 by Thomas Laxton, of Bedford, England. Thereafter intensive use of crossing served to incorporate the desired colors in the commercial grandiflora, hooded, and Spencer types and to vary the color and form of blooms in the important winter-flowering group. The number of favorable mutations occurring in the sweet pea in two centuries of culture is truly remarkable. These have served as the material from which practical breeders have constructed the varied horticultural varieties of our day.
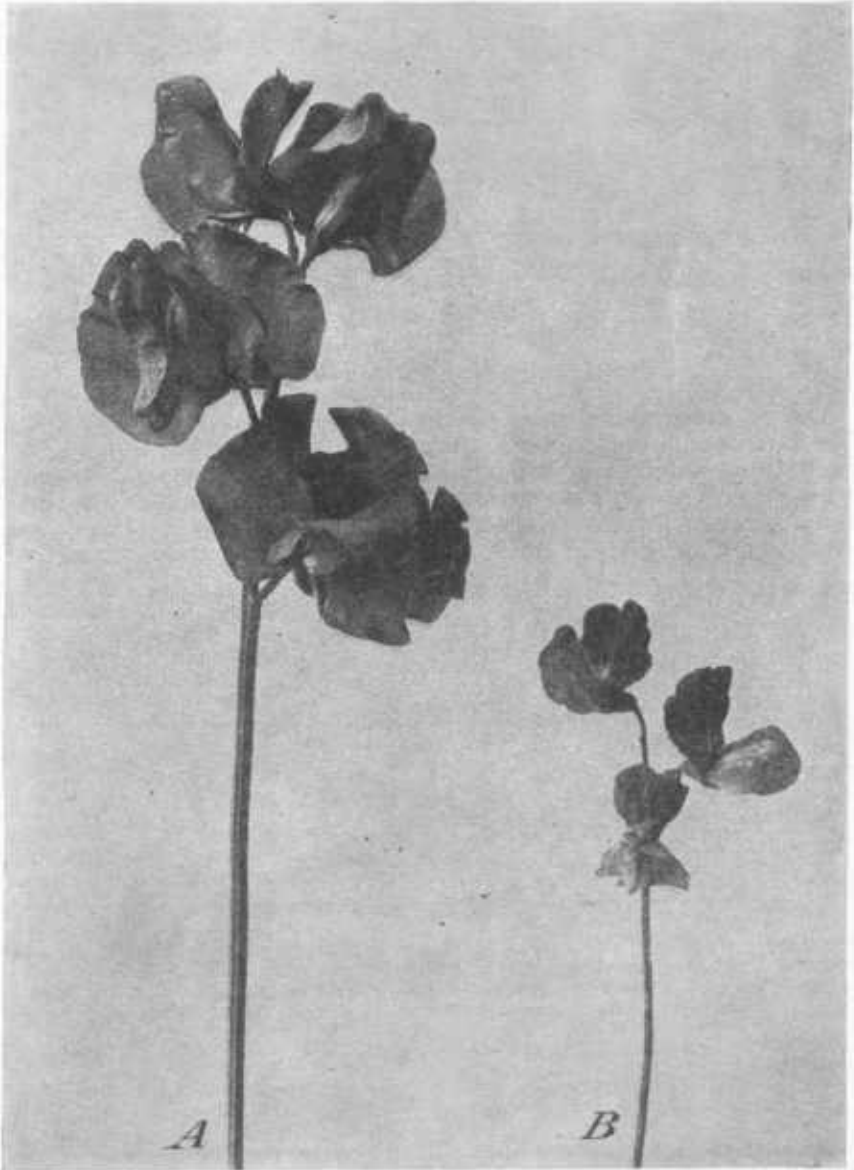
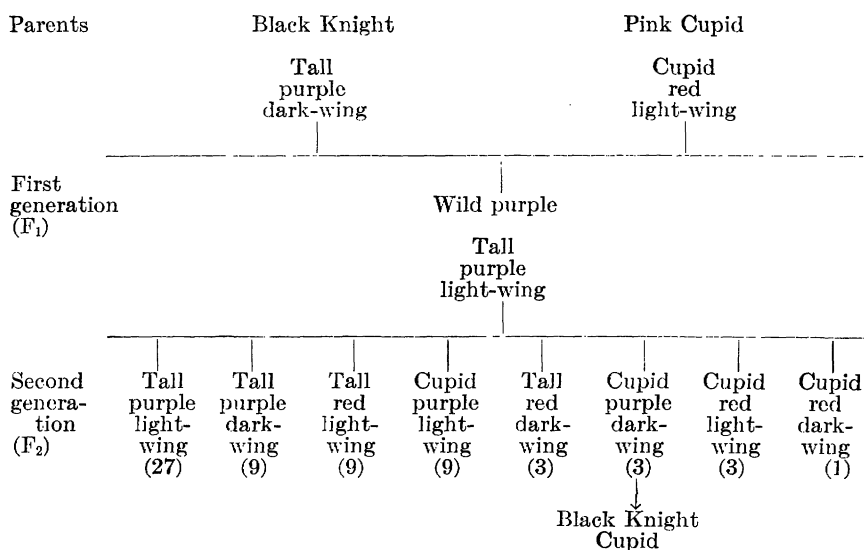Figure 25.—A modern sweet pea (A) and a type closely resembling the wild form (B), from which it arose. The greatest part of this development has taken place in the last 25 years.

Hurst (223) has presented some examples of the actual procedure followed in producing new combinations by hybridization. W. Cuthbertson produced the Waved King Edward variety as follows.

Parents	King Edward		Countess Spencer
	Plain red		Waved pink

| First generation (F₁) | | Plain red | |

| Second generation (F₂) | Plain red (9) | Plain pink (3) | Waved red (3) | Waved pink (1) |

Waved King Edward

The expected proportions of the F_2 population are supplied by Hurst since Cuthbertson did not count the classes. Out of the desired waved red class in F_2, one-third of the plants should be pure breeding and two-thirds segregating again 3 red : 1 pink. Cuthbertson also raised Primrose Spencer by a similar procedure. Hurst also explains the synthesis of Black Knight Cupid in his own experiments:

Parents	Black Knight	Pink Cupid
	Tall purple dark-wing	Cupid red light-wing

| First generation (F₁) | Wild purple |

Tall
purple
light-wing

| Second genera- tion (F₂) | Tall purple light- wing (27) | Tall purple dark- wing (9) | Tall red light- wing (9) | Cupid purple light- wing (9) | Tall red dark- wing (3) | Cupid purple dark- wing (3) | Cupid red light- wing (3) | Cupid red dark- wing (1) |

Black Knight
Cupid

Black Knight Cupid was then "fixed" by saving the progeny of the one-third of this class that were true breeding, and discarding the two-thirds that segregated in the third generation into 3 purple : 1 red. The synthesis of combinations in this manner is simple when the desired genes are available in different varieties and their mode of inheritance is known.

In addition to the many valuable mutations that have made possible the range in color and form of modern sweet pea varieties, other mutations of minor value and actually harmful types have

appeared. Among the mutant forms of minor or novelty interest may be mentioned the "snapdragon" type in which the standard is folded around the wings. This is inherited as a simple recessive to the normal type. Recently Wright has described a variety producing two or even three flower stalks at each node, without loss of size or beauty of the flowers. This may be regarded as a new mutant, evidently of minor commercial value, for no further reference to it has appeared. The change from "long" pollen to "round" is an example of a mutant neither useful nor harmful from the horticultural viewpoint, while "contabescent" anthers, a recessive mutant bearing abortive anthers, and the monstrous "cretin" type with abortive pistil, illustrate harmful mutants. Stone's report of a somatic mutation from recessive cupid to normal tall illustrates that the mutation process is still active in sweet peas.

Although hybridization has been widely employed, natural crossing between varieties of sweet peas is probably infrequent. Until recently there was no authentic record of a successful cross of *Lathyrus odoratus* with any other species of the genus. Barker (*11*) reports success with only one cross between species out of many attempted. This hybrid, *L. odoratus* Kitty Clive × *L. hirsutus* (a weak annual), was fertile; segregation occurred in the second hybrid generation, but the *L. odoratus* type was not recovered. No noteworthy ornamental type appeared in this or later generations. A few seeds were obtained on pollinating the first-generation hybrids from *L. odoratus* × *hirsutus* with pollen from one of the perennial species of *Lathyrus*.

The modern sweet pea leaves little to be desired in form of flower and variety of color. A true yellow is not available though long sought, and brighter shades of present colors are still desired, as well as reds and pinks that do not sunburn. The duplex type, a recent novelty with extra petals producing the effect of added size of bloom, seems worthy of fixing and of hybridizing to extend the range of color and types available. Resistance to diseases, particularly of the root rot group, is needed. A hardier race of sweet peas to endure winter cold and permit fall planting and one enduring summer heat would serve to extend the range of satisfactory garden culture of this excellent annual.

LITERATURE CITED

Literature citations for this article, covering 564 references on flower breeding, are omitted from this volume because of space limitations but are available in the 1937 Yearbook Separate on Improvement of Flowers by Breeding.

APPENDIX

SUPPLEMENTARY DATA ON LILY BREEDING

Classification of the species Lilium

Subgenus *Eulirion:* True lilies. Bulb perennial; leaves linear, lanceolate or lanceolate-ovate.

    Section 1. Leucolirion: Trumpet lilies. Flowers trumpet-shaped, horizontal or nodding; perianth segments falcate or spreading at the apex; stamens not divergent.

        Examples: *Lilium candidum* L., *L. formosanum* Stapf., *L. longiflorum* Thunb., *L. regale* Wils.

    Section 2. Archelirion: Lilies with open, bowl-shaped flowers. Perianth segments widely spreading, broadest below the middle; stamens divergent.

        Examples: *L. auratum* Lindl. only, according to Wilson; but also *L. speciosum* Thunb. and *L. tigrinum* Ker according to Baker. Grove adds *L. henryi* Baker and *L. leichtlinii* Hook. f. and comments that the dividing line between Archelirion and Martagon is arbitrary and may need revision.

    Section 3. Isolirion: Lilies with erect flowers. Perianth segments falcate, not revolute at apex. Leaves whorled or scattered. Stamens divergent.

        Examples: *L. bulbiferum* L., *L. philadelphicum* L., *L. concolor* Salisb.

    Section 4. Martagon: Lilies with nodding flowers and strongly revolute perianth parts. Leaves whorled or scattered. Stamens divergent. The Turkscap group.

        Examples: *L. martagon* L., *L. chalcedonicum* L., *L. hansoni* Leicht., *L. amabile* Palibin, *L. cernuum* Komarov, *L. superbum* L., *L. willmottiae* Wils.

Subgenus *Cardiocrinum:* Heart-leaved lilies. Bulbs monocarpic (flowering only once); leaves long-petioled, ovate-cordate.

    Examples: *L. cordatum* (Thunb.) Koidz., *L. giganteum* Wallich.

List of Lily Hybrids Arranged in Alphabetical Order of the Seed Parents

Species names of the seed parents are followed by the author of the name, the date the name was assigned, the section in which the species is usually placed, and the region to which the species is native. Under the seed-parent headings are listed the pollen parents reported to cross, named hybrids, if any, in quotation marks, and sometimes comment on the results. The practice of indicating a hybrid species by inserting the sign of multiplication (×) before the species name, as *L.* × *testaceum*, has been followed.

Lilium amabile Palibin, 1901. Martagon. Chosen.
    × *L. martagon.* Preston reports one success.
L. auratum Lindley, 1862. Archelirion. Japan.
    × *L. speciosum* var. *melpomene* = "*L.* × *hoveyi.*"
    × *L. speciosum* (?) = "Mrs. Anthony Waterer."
    × *L. speciosum.* Preston reports success.
L. auratum var. *platyphyllum* Baker, 1880. Archelirion. Japan.
    × *L. speciosum* var. *magnificum* = "*L.* × *parkmanni* var. *haywardi.*"
    × *L. speciosum* var. *melpomene* (?) = "*L.* × Crimson Queen."
    × *L. speciosum.* Stout reports success.
L. auratum var. *rubrovittatum* Duchartre, 1870. Archelirion. Japan.
    × *L. auratum.* Stout reports success.
L. bulbiferum L., 1753. Isolirion. Europe.
    × *L. croceum* (syn. *L. bulbiferum* subsp. *croceum*). Griffiths reports one worthy hybrid.
    × *L.* × *thunbergianum* (syn. *L.* × *elegans*). Berckmüller reports many crosses. According to him the varieties *incomparabile, erectum, grandiflorum, multiflorum,* and Sappho of *L.* × *umbellatum* of commerce are referable to the cross *L. bulbiferum* × *L.* × *thunbergianum.* Berckmüller

further suggests that the name *L. umbellatum* should be restricted to the progeny of this cross and that a new name should be created for those newer varieties of *L. × umbellatum* of commerce that are referable to the cross *L. croceum × L. × thunbergianum*.

L. bulbiferum subsp. *croceum* (Chaix) Baker, 1873. Isolirion. Europe.
× *L. concolor*. Preston reports one success.
× *L. dauricum*. Stout reports success.
× *L. davidi*="*L. × crovidi*." *L. × crovidi × L. × cromottiae*="*L. ×* Golden King*.*"
× *L. × elegans*="*L. ×* Coolhurst hybrid."
× *L. × elegans*. Preston and Stout report successes.
× *L. tenuifolium* (syn. *L. pumilum*). Preston reports two natural hybrids.
× *L. × thunbergianum* (syn. *L. × elegans*). Berckmüller reports many successes and from the resemblance of the progeny to such newer varieties of *L. × umbellatum* of commerce as Golden Fleece, Orange King, Invincible, Splendidum, Mahogany, and Vermilion Brilliant, he considers that a new name should be created for this cross, reserving the name *L. × umbellatum* for the cross *L. bulbiferum × L. × thunbergianum*.
× *L. tigrinum*="*L. × manglesi*."
× *L. willmottiae*="*L. × cromottiae*."

L. canadense L., 1753. Martagon. Eastern America.
× *L. grayi*. Stout reports success.
× *L. superbum*. Stout reports success.
× *L. tenuifolium* (syn. *L. pumilum*). Preston reports success.

L. candidum L., 1753. Leucolirion. Europe to Western Asia.
× *L. chalcedonicum*. Griffiths reports promise.
× *L. parryi*. Grove reports success in 1914.
× *L. × testaceum*. Preston reports success.
× *L. × testaceum*. Griffiths reports success but no hybrids of promise.

L. chalcedonicum L., 1753. Martagon. Greece.
× *L. candidum*=*L. × testaceum*, natural hybrid (1830?). It is generally agreed that *L. testaceum* is of this origin, but the exact time and place of origin are uncertain. Hybrids closely resembling *L. testaceum* have been reproduced at least three times.

L. concolor Salisbury, 1806. Isolirion. China.
× *L. dauricum*="*L. × elegans*." Berckmüller produced this cross and found the progeny conformed to the description of *L. thunbergianum* Schultes. The latter species is therefore presumably a hybrid and synonymous with *L. × elegans*.
× *L. tenuifolium* (syn. *L. pumilum*). One success by Van Fleet, according to Griffiths.

L. dauricum Ker, 1809. Isolirion. Northeastern Asia.
× *L. croceum* (syn. *L. bulbiferum* subsp. *croceum*), Stout reports success.
× *L. × elegans*. Stout reports success.
× *L. × thunbergianum* (Syn. *L. × elegans*). Preston flowered seedlings.
× *L. × umbellatum*. Preston flowered seedlings.

L. davidi Duchartre, 1880. Martagon. China.
× *L. pseudotigrinum* (?). Preston reports success.
× *L. tigrinum* var. *fortunei*. Preston reports success. (Probably *L. tigrinum* var. *diploid*.)
× *L. willmottiae* = "*L. × davmottiae*." Preston states that the cross *L. davidi* (the *sutchuenense* form) × *L. willmottiae* was made in 1922. A number of seedlings sent out as "Ottawa hybrids" were later called *davmottiae*, which has resulted in lack of uniformity.

L. × elegans Thunberg, 1811. Isolirion hybrid. Japan. Not known wild. Berckmüller has shown that *L. elegans* Thunberg (syn. *L. thunbergianum* Schultes) is a hybrid, *L. concolor × L. dauricum*.
× *L. croceum*. Preston and Stout report success.
× *L. dauricum*. Stout reports success.
Preston reports *L. × thunbergianum × L. dauricum* successful

L. grayi S. Watson, 1879. Martagon. Eastern United States.
× *L. canadense*. Stout reports success.

L. hansoni Leichtl., 1874. Martagon. Northeastern Asia.
× *L. × dalhansoni*. Preston reports success.
× *L. × marhan*. Preston reports success.

× *L. martagon.*   Griffiths reports interesting seedlings.
× *L. martagon album* "*L.* × St. Nicholas."   Preston also reports success.
× *L. medeoloides* (?).   Stout reports success.
× *L. tenuifolium* (syn. *L. pumilum*).   Stout reports 42 pollinations failed,
   40 yielded capsules, only 3 seeds germinated.
L. henryi Baker, 1888.   Martagon.   China.

× *L. auratum*
× *L. candidum*
× *L.* × *princeps* seedling
× *L. regale* }Preston reports success.
× *L. speciosum*
× *L.* × *testaceum*
× *L. tigrinum*

× *L. leucanthum* var. *chloraster* = "*L.* × *kewense.*"
× "3 Asiatic Martagons" successful according to Griffiths.
× *L. sutchuenense* (?).   Stout reports that plants from bulbs received from
   C. P. Horsford under this name were self-fertile and fertile with *L. will-
   mottiae* pollen.
L. humboldtii Roezl. and Leichtl., 1871.   Martagon.   California.

× *L. parryi* {"Frances Larrabee"
            "Mercer Girl"
            "Vashon"

L. humboldtii var. *bloomerianum* (Kellogg) Jepson, 1922.   Martagon.   California.

× *L. humboldti* var. *magnificum*}
× *L. parryi* (?) }Stout reports success.
× *L. roezli*

L. humboldtii var. *magnificum* Purdy, 1897.   Martagon.   California.

× *L.* × Amos Perry = "*L.* × *gloriosum.*"
× *L. humboldti* var. *bloomerianum*}
× *L. roezli* }Stout reports success.

× *L. pardalinum* Kellogg.   "Cyrus Gates", "Douglas Ingram", "John
   McLaughlin", "Kulshan", "Sacajawea", "Shuksan", "Star of Oregon."
   These are all F$_1$ seedlings from Griffiths' crosses.   Further lines of gar-
   den merit were expected from intercrossing and backcrossing these.
L. kelloggii Purdy, 1901.   Martagon.   California.

× *L. canadense*
× *L. humboldti*
× *L. parryi* }Feeble fertility is reported by Stout.
× *L. parvum*
× *L. roezli*

L. leichtlinii var. *maximowiczii* (Regel) Baker, 1871.   Martagon.   Eastern Asia.
× *L. dauricum* var. *venustum* f. *batemanniae* = "*L.* × *horsfordi.*"   Griffiths
   also reports a hybrid worth introducing.
× *L. tigrinum.*   Preston reports one success.
× *L. willmottiae* = "*L.* × Maxwill."
L. leucanthum Baker, 1901.   Leucolirion.   China.

× *L.* × George C. Creelman]
× *L. regale* }Griffiths reports successful crosses, the first
× *L. sargentiae* }   two yielding promising hybrids.

L. leucanthum var. *chloraster* (Baker) Wilson, 1925.   Leucolirion.   China.
× *L. regale* = "*L.* × *centigale.*"
× *L. sulphureum* (syn. *L. myriophyllum* var. *superbum*).
L. longiflorum Thunberg, 1794.   Leucolirion.   Eastern Asia.
× *L. regale.* Preston reports one success.
L. × *marhan* (*L. martagon* var. *album* × *L. hansoni*).   The Netherlands, 1886.

× *L.* × *dalhansoni*
× *L. hansoni* }Preston reports successes.
× *L. martagon* var. *album*

L. martagon L., 1753.   Martagon.   Europe and Asia.
× *L. hansoni.*   Stout reports success.
L. martagon var. *album* Hort., 1880.
× *L. hansoni* = "*L.* × *marhan.*"   The varieties "Ellen Willmott" and
   "E. J. Elwes" were derived from "*L.* × *marhan.*"

× *L. bolanderi* S. Wats.
× *L. callosum* Sieb. and Zucc.
× *L. carniolicum* Bernh.
× *L. columbianum* Hanson
× *L. davidi*
× *L. grayi* S. Wats.
× *L. kelloggi* Purdy
× *L. maritimum* Kellogg
× *L. medeoloides* A. Gray
× *L. pardalinum* Kellogg
× *L. willmottiae*

} Grove reports successful crosses but no progeny of note.

L. martagon var. *dalmaticum* Elwes, 1877.
  × *L. hansoni* = "*L.* × *dalhansoni.*"
  × *L. medeoloides* = "*L.* × *Marmed.*"
L. martagon and varieties.
  × *L. hansoni* = "Backhouse hybrids": "Brocade", "Golden Orb", "Mrs. R. O. Backhouse", "Sceptre", "Sutton Court", etc.
L. myriophyllum var. *superbum* (Baker) Wilson, 1925. Leucolirion. Upper Burma. (Syn. *L. sulphureum* Baker 1892.)
  × *L. regale* = "*L.* × *sulphurgale.*"
  F₂ seedlings are also sold as "*L.* × *sulphurgale.*"
  L. × *sulphurgale* × *L.* × *princeps* = "Crow's Hybrid."
L. neilgherrense Wight, 1853. Leucolirion. Southern India.
  × *L. wallichianum* = "*L.* × *burnhamense.*"
L. pardalinum Kellogg, 1863. Martagon. California, Oregon.
  × *L. humboldti* = "*L.* × *pardaboldti.*" "Dimsdale variety" is a selection from the hybrid.

× *L. washingtonianum* Kellogg
× *L. humboldti*
× *L. parryi*
× *L. maritimum*

} Purdy believes that Luther Burbank's hybrids fall into these four groups, and an additional untraceable group. Many other species crosses were attempted but not kept separated. Some excellent types were produced but L. *burbanki*, which bears the originator's name, is "a nondescript medley"—Purdy.

  × *L. columbianum.* Considered promising by Griffiths.
  × *L. superbum.* Successful but not promising.—Griffiths.
L. parryi S. Wats., 1878. Leucolirion. California.
  × *L. humboldti* var. *magnificum* = "*L.* × Amos Perry."
  × *L. pardalinum* = "*L.* × *burbanki.*"
              = "Napier's variety."
              = "*L.* × Frances Fell."
              = "*L.* × Peter Puget." Grove states this cross yields fine hybrids, some of which are yellow-flowered.
  × *L. parvum* var. *luteum* = "*L.* × *roemeri.*"
L. parvum Kellogg, 1863. Martagon. California, Oregon.
  × *L. pardalinum*⎰ According to Grove these hybrids are attractive but lack
  × *L. parryi* ⎱ "staying power."
L. philadelphicum L., 1762. Isolirion. Eastern North America.
  × *L. dauricum* = "*L.* × *phildauricum.*" Skinner discusses his recent crosses in a letter to Preston.
L. pseudotigrinum (?).
  × *L. callosum.* Preston reports one success.
L. pumilum DC., 1813. Martagon. Northeastern Asia. (Syn. *L. tenuifolium* Fischer 1812.)
  × *L. martagon album*="*L.* × Golden Gleam." According to Grove, "Golden Gleam" was originally an authentic hybrid but has since been propagated by seed.
  × *L.* × *elegans*
  × *L. martagon*
  × *L. martagon* var. *album*
  × *L. regale*
  × *L. speciosum*
  × *L.* × *testaceum*

} Preston reports successful crosses.

× *L. chalcedonicum* ⎤
× *L. monadelphum* ⎬Skinner reports successful crosses.
× *L. regale* ⎦

L. regale Wilson, 1912.   Leucolirion.   China.
  × *L. tenuifolium.*   Claimed by Theodore Albert.
  × *L. auratum* ⎤
  × *L. candidum*
  × *L. longiflorum*
  × *L. speciosum* var. *rubrum* ⎬Preston reports successful crosses.
  × *L.* × *sulphurgale*
  × *L.* × *testaceum*
  × *L. tigrinum* ⎦
  ×*L. sargentiae* ⎤
  × (*L. sargentiae* × *L. regale* seedling)⎬Stout reports success.
  × *L.* × George C. Creelman.
  × *L. leucanthum* ⎤
  × *L. sargentiae* ⎬Griffiths reports successful crosses.
  × *L. sulphureum*
  × *L.* × *sulphurgale*⎦
  × *L. browni* ⎬Griffiths mentions possible successes.
  × *L. longiflorum*⎦

L. roezli Regel, 1870.   Martagon.   California.
  × *L. parryi.*   Grove records a fine hybrid of good constitution.
  × *L. columbianum* ⎤
  × *L. humboldti* ⎬Stout reports success.
  × *L. parryi* ⎦

L. sargentiae Wilson, 1912.   Leucolirion.   China.
  × *L. henryi* = "*L.* × *aurelianense.*"
  × L. × *aurelianense.*   Debras reports seedlings growing, also seedlings of "*L.* × *aurelianense*" selfed.
  × *L. regale* = *L.* × *princeps* (syn. "*L.* × *sargale*").   First appeared as a chance seedling.   J. W. Crow had some interesting seedlings from the cross *L.* × *princeps* × *L.* × *sulphurgale.*
    = "*L.* × George C. Creelman."
    = *L.* × Pride of Charlotte.   This hybrid is reported to come true from seed.   Preston and Stout also report successful crosses.
  × *L.* × *aurelianense.*   Debras reports success.

L. speciosum Thunberg, 1794.   Martagon.   Japan.
  × *L. auratum.*   Preston and Stout report successes.
  × *L. candidum* ⎤
  × *L. henryi*
  × *L. regale*
  × *L. speciosum* var. *album* ⎬Preston reports successful crosses
  × *L.* × *testaceum*
  × *L. tigrinum* ⎦
  × *L. tigrinum* seedling raised by Crow did not reach flowering size.

L. speciosum var. *album* Hort.
  × *L. tigrinum.*

L. speciosum var. *magnificum* Hort.
  × *L. speciosum* var. *melpomene.*   Remarkable hybrid.   Griffiths.
  × *L. regale* ⎬Early crosses were successful but seedlings were lost.   Preston
  × *L. tigrinum*⎦

L. speciosum var. *rubrum* Hort.
  × *L. auratum* = "*L.* × *parkmanni.*"
  × *L. tigrinum.*   Preston reports early seedlings were lost.

L. superbum L., 1762.   Martagon.   Eastern North America.
  × *L. canadense*⎬Stout reports success.
  × *L. roezli* ⎦

L. × *testaceum* Lindl., 1845.   This hybrid, *L. chalcedonicum* × *candidum*, was first recognized in Germany in 1836 and probably originated in the Netherlands about 1830.
  × *L. candidum*="White Knight."   Preston and Stout also report success.
  × *L. chalcedonicum*="*L.* × *beerensi.*"   Griffiths reports this cross promising.

L. tigrinum Ker, 1810.   Martagon.   Eastern Asia.
    $\times$ *L. elegans* var. *wallacei* (syn. *L. dauricum* var. *wallacei* (Wallace) Wilson).
      Stout reports success.
    $\times$ *L. leichtlini* var. *maximowiczi* = "*L.* $\times$ *tigrimax.*"   Stout also reports
      success.
    $\times$ *L.* $\times$ *tigrimax.*   Preston reports success.   Stout reports success with pollen
      of the F_1 hybrid *L. tigrinum* $\times$ *maximowiczi.*
    $\times$ *L. sutchuenense.*   Stout reports success.
    $\times$ *L. willmottiae.*   Preston has flowered seedlings.
L. tigrinum var. *fortunei* Hort., 1866.   Preston describes a form of *L. tigrinum*
  referred to this variety by Wilson, which is self-fertile.   In a recent paper
  Preston names this form *L. tigrinum* "var. diploid."
    $\times$ *L. auratum* $\Big\}$ Preston reports success.
    $\times$ *L. leichtlini* var. *maximowiczi*
L. $\times$ *umbellatum* Hort., 1874.   Berckmüller considers that this form is a hybrid—
  L. bulbiferum $\times$ *L.* $\times$ *thunbergianum* (*L.* $\times$ *elegans*).   The name *L. umbellatum*
  has been used by Dutch hybridizers for various hybrid lilies of the upright-
  flowered type.
    $\times$ *L. bulbiferum.*   Griffiths reports one seedling of merit.
    $\times$ *L.* $\times$ *willcrovidi* = "*L.* $\times$ Fire King."
L. willmottiae Wils., 1913.   Martagon.   China.

    $\times$ *L.* $\times$ *crovidi* = "*L.* $\times$ *willcrovidi.*"
    $\times$ *L. dauricum* seedling = "*L.* $\times$ Grace Marshall"
                                "*L.* $\times$ Lila McCann"
                                "*L.* $\times$ Lilian Cummings" $\Big\}$ Preston.
                                "*L.* $\times$ Phyllis Cox"
    $\times$ *L.* $\times$ *elegans* "Mahogany" = "*L.* $\times$ *scottiae.*"
    $\times$ *L. davidi*
    $\times$ *L. grayi*
    $\times$ *L. speciosum* $\Big\}$ Preston reports successes.
    $\times$ *L. tigrinum* var. *fortunei*
    $\times$ *L.* $\times$ *umbellatum*
    $\times$ *L. tigrinum*
    $\times$ *L. pseudotigrinum* $\Big\}$ Stout reports successes.
    $\times$ (*L. henryi* $\times$ *L. sutchuenense*)
    $\times$ *L. farreri*
    $\times$ *L. monadelphum* $\Big\}$ Successful crosses reported by Skinner.
    $\times$ *L. regale*
    $\times$ *L. washingtonianum*

GENETIC STUDIES ON ORNAMENTAL PLANTS

    The utilization of genetic science in practical breeding of flowers is in its infancy.
The following brief survey indicates the scope of genetic work on ornamental
plants.   It will be noted that the characters studied are often of little floricultural
interest, and that plants of minor ornamental value have received attention, while
many flower favorites have been nearly or wholly ignored.   The object of genetic
research has been largely to extend knowledge of the operation of the laws of
heredity.   Ornamental plants have been studied chiefly because they offer easily
recognizable characters, and because they are convenient to grow.
    The material assembled here is necessarily brief.   No claim to completeness is
made.   Those interested in specific plants will usually find further details in the
original publications cited in the bibliography, which appears in the 1937 Year-
book Separate, Improvement of Flowers by Breeding.   References are indicated
by italic figures following the names of authors in parentheses.   Much of the
literature up to 1929 is covered by Matsuura (*339*), and up to 1930 by Warner,
Sherman, and Colvin (*532*).
Abutilon.   (Klebahn, *301*.)
    In crosses between *Abutilon striatum* and *A. thompsoni* flower and leaf char-
acters proved hereditary.   A range of color shades in F_1 suggested hybridity
in the parents.   The F_1 proved largely sterile.
Althaea.   (Saunders, *458*.)
    In a cross of double-flowered $\times$ single-flowered the F_1 was intermediate; the
F_2 ratio was 1 single: 2 intermediate: 1 double.
Amaranthus caudatus L.   (De Vries, *530*.)
    The red-leaved type is dominant to the green.

Anagallis arvensis L.   (Heribert-Nilsson, *200;* Weiss, *538.*)
    Scarlet-flowered × blue produced scarlet flowers in F_1; in F_2 scarlet and blue in no usual Mendelian ratio.   Pink (nearly white) × red-flowered yielded red flowers in F_1; in F_2, 3 red : 1 pink-flowered.
Anemone.   (Hildebrand, *204;* Rosén, *442, 444.*)
    Dark-blue flower color (*Anemone hepatica*) × white (*A. acutiloba*) produced light blue in F_1.   Light blue (*A. angulosa*) × dark blue produced an intermediate color in F_1.   Blue and red are dominant to white.   Red × white often yielded blue in F_1, and in F_2 a ratio of 9 blue : 3 red : 4 white.
Antirrhinum calycinum Lam.   (Saunders, *462.*)
    Red corolla color is dominant to white, and glabrous stems and capsules to hairy.   In the F_1 of red × white corolla, the red color is both diluted and retarded, i. e., the flowers developed in later growth are deeper red than early flowers of the same plant.
Antirrhinum hispanicum Chav.   (Baur, *34;* Filzer, *128;* Sirks, *484.*)
    In a cross between two self-sterile plants, the F_1 was divisible into two classes, one fertile with either parent, the other with one parent only.   Filzer explained Baur's data by assuming three genes for sterility, one of which was common to the two parents.
Antirrhinum majus L.   (Bateson, *16;* Baur, *27, 28, 29, 30, 31, 32, 33, 35, 36, 37, 38, 39;* Gairdner and Haldane, *140;* Hackbarth, *160;* Hertwig, *201;* Herzberg-Fränkel, *202, 203;* Hiorth, *208;* Kuckuck, *306;* Saulescue, *448;* Scherz, *468;* Schiemann, *469;* Stein, *492, 493;* Stubbe, *499, 500, 501;* De Vries, *529;* Wheldale, *541, 542, 543.*)
    Research has given information about some 200 genes in this plant.   Color inheritance is complex.   Wheldale interprets color expression on the basis of at least seven interacting genes.   Baur adds to these a number of basic genes further conditioning, modifying, or intensifying color expression.   Baur and his students and others have studied in a large number of mutants the inheritance of form of flower, form of and color distribution in leaves, and stem peculiarities.   Most of these mutants, which appeared spontaneously in Baur's cultures, are defective types, and all but one, "crispa" (conditioning wavy leaf margins), are recessive.   "Crispa" is dominant, distinctly deleterious in the heterozygous condition, and lethal when homozygous.   Mutations have been artificially induced in snapdragon by treatments with radium (Stein), X-rays, ultraviolet light, and temperature shocks (Stubbe).   Dwarfs and leaf defects are common; all the induced mutants are inferior types.   In general the mutants are similar to spontaneous mutants but appear in higher frequencies.   Stubbe records the appearance of some mutants not observed previously, and Stein reports a tendency to gall formation induced by radium.   Baur found chemical treatment of stem tips ineffective, and Hiorth obtained no gene mutations from heat-treated pollen grains.
    Several instances of linkage have been determined in the snapdragon.   Gairdner and Haldane have reported a case of balanced lethals, i. e., two closely linked genes, each causing death of the individual when homozygous, permitting a heterozygous plant to breed nearly true, through elimination of the two homozygous classes.
Antirrhinum species hybrids.   (Baur, *34;* Brieger, *55;* Gruber, *156;* Gruber and Kühl, *157.*)
    Baur has studied the inheritance of fertility and sterility in several species of *Antirrhinum*.   *A. ibanyezi, A. molle, A. glutinosum, A. hispanicum*, etc., are fully self-sterile; a form of *A. majus* is fully self-fertile.   Crosses between self-sterile and self-fertile forms yielded in F_2, 15 self-fertile : 1 self-sterile.   Gruber's and Brieger's results indicate that the inheritance of sterility is often more complex.   Gruber and Kühl found the radial (peloric) flower character linked with genes for self-sterility.
Aquilegia vulgaris L.   (Baur, *30, 32;* Brieger, *54;* Kristofferson, *304.*)
    On selfing a dark blue plant, Kristofferson obtained a ratio of 9 dark blue : 3 red : 3 light blues : 1 white.   Two genes were assumed, one having additional effects on plant color extension, producing self-color when dominant and white-margined when recessive.   Baur found two types of chlorophyll defects— "chlorina" (yellowish green) and "variegata" were each monogenic recessive to the normal green.   Chlorina is also a monogenic recessive to variegata.   Brieger found flower colors segregating in the pattern of 9 blue : 3 red : 4 white,

with modifying genes controlling intensity of color. Spurless is determined by two polymeric dominants over spurred.

Aquilegia species hybrids. (Anderson and Schafer, *5, 6;* Blaringhem, *51;* Skalińska *487.*)

Anderson and Schafer found wide petals dominant over narrow and medium length spurs over very long or very short ones in first-generation species hybrids. They observed 16 percent of natural crossing between two strains of *Aquilegia vulgaris*, but none between *A. vulgaris* and *A. skinneri.* Skalińska reports that anthocyanin flower color is linked with straight spurs. *A. californica* × *A. flabellata* yields a fertile F_1 generation and shows both parental types in F_2. The reciprocal cross differs in F_1 and shows no paternal type in F_2. Blaringhem has reported on inheritance in crosses of a mutant type having only female flowers with normal *A. vulgaris*, and also with *A. sibirica* and *A. chrysantha.*

Arabis albida Stev. (Correns, *97.*)

Correns studied three types of periclinal chimaeras in this plant. One type, "leucodermis", is inherited only through the female parent, not through the pollen (maternal inheritance); the other two types are Mendelian recessives.

Argemone. (Correns, *85;* Meunissier, *344.*)

Yellow-flowered *Argemone mexicana* × pale yellow *A. ochroleuca* yielded F_1 plants of intermediate color. *A. mexicana* × *A. platyceras* (white-flowered) produced plants of intermediate type in F_1, and in F_2 a new color type and several new forms in other characters.

Arum maculatum L. (Colgan, *77.*)

Colgan raised 11 seedlings from a plant having black spots on the leaves; of these 5 bore spotted leaves, 6 lacked spots.

Aster tripolium L. (Fleming, *131.*)

Fleming reports that purple flower color is dominant to pink and that pink is dominant to white.

Atropa belladonna L. (Bateson and Saunders, *23.*)

Differences in color of flowers, fruits, and stems, which distinguish the variety *lutea* from the type of the species, showed monogenic inheritance.

Barbarea vulgaris R. Br. (Anderson, *7;* Dahlgren, *105.*)

One type of variegation shows maternal inheritance only. Another type differs from the normal green type by duplicate recessive genes. Somatic segregation also occurs.

Begonia. (Bateson and Sutton, *26.*)

Inheritance of double versus single flowers showed irregularities not fully accounted for.

Bryonia dioica Jacq. (Jones and Rayner, *275.*)

Absence of bloom on the berry proved to be a monogenic dominant to its presence. In a cross between a variety with deeply lobed, rough, dark-green leaves and a variety with less deeply lobed, smoother, and paler leaves, the F_1 was intermediate, and new types appeared in the F_2 population. Number of carpels and number of vascular bundles in the stem were also studied.

Callistephus. (Fleming, *131.*)

From the results of natural crossing it is inferred that purple flower color is dominant to red, and red to white. Deep pink is dominant to white.

Campanula carpatica Jacq. (Pellew, *403, 404.*)

Blue flower color is a simple dominant to white, but irregular segregation occurs in formation of the pollen grains, so that 97 percent carry the gene for blue, and only 3 percent carry the gene for white. Paler shades of blue are usually recessive to darker shades. White or "patched" seedlings proved recessive to the normal green type.

Campanula medium L. (Correns, *87;* Lathouwers, *309.*)

The "hose-in-hose" or "cup and saucer" type with petaloid calyx proved to be a partial dominant to the normal. In F_2 a ratio of 3 "hose-in-hose": 1 normal appeared. Lathouwers also crossed rose-flowered × white; the F_1 generation was dark violet; in F_2 segregation occurred in the ratio of 9 colored: 7 white, the colored forms falling into the ratio of 9 dark violet: 3 violet: 3 lilac: 1 rose-flowered. This was interpreted on the basis of two complementary genes for formation of anthocyanin and two further genes for color singly conditioning lilac and violet, and together producing dark violet, with rose the double recessive.

Campanula persicifolia L.   (Bateson, *18*.)

A dwarf form very distinct from the normal type in appearance proved to be a monogenic recessive to the normal.

Canna.   (Honing, *213, 214, 215, 216, 217*.)

Honing studied the behavior of some 18 genes in *Canna glauca, C. indica*, and in segregates from crosses between these species.   The inheritance of red leaf margin is complex; in one cross the presence of three complementary genes was indicated, in other crosses monogenic and digenic ratios appeared.   A monogenic difference was found responsible for the deep scarlet flower color of *C. indica* as contrasted with yellow flowers of *C. glauca*.   Further studies of intensity of flower color, flaking in the flowers, etc., indicated that several genes were involved with ratios disturbed by linkages and lethal genes.   Other characters of staminodes, leaves, stems, fruits, seeds were studied.

In crosses of *Canna indica* and *C. aureo-vittata* the proportion of red-margined leaves in the progeny is said to be influenced by differential growth rates of pollen tubes of differing genetic constitution, and also by the constitution of the plasma, so that reciprocal crosses may differ, particularly with respect to the proportions of plants with red-margined leaves.   The appearance of a giant type as a somatic mutation is recorded.

Cattleya.   (Hurst, *222, 223, 224;* Reychler, *436;* Reychler and Kamerling, *437*.)

In crosses of various Cattleya species, rosy purple flower color proved dominant to white, with two complementary genes involved.   Certain albinos therefore produced colored forms on crossing.   Other albinos behaved as monogenic recessives to colored.   The yellow color of *Cattleya dowiana* var. *aurea* is recessive to the rosy purple color; yellow color in other cattleyas is partially dominant to rosy purple.   Reychler mentions a collection of 175 seedlings derived from a cross of two mutants of *C. labiata*.

Celosia cristata L.   (Kanna, *282;* Kihara, *300;* Terasawa, *507*.)

"Mosaic" inflorescence (a mixture of red and yellow) yielded on selfing a few reds in addition to the mosaic type.   On selfing these reds a ratio of 3 red: 1 mosaic resulted.   Kanna also found red dominant to mosaic.   In his mosaic lines two types of bud variations were noted.   A series of four multiple allels governs flower color (yellow or red) and stem color (green or red).   Striping is produced by a recessive gene, which may mutate to the dominant colored condition.

Centaurea cyanus L.   (Mekel, *341*.)

A system of three genes is presented to explain inheritance of blue, pink, and white flower color.

Cheiranthus cheiri L.   (Blaringhem, *50;* Nelson, *388;* Sirks, *481*.)

The abnormal form *Cheiranthus cheiri* var. *gynanthus*, in which stamens are replaced by extra carpels and petals are much reduced, is a monogenic recessive to normal.   In flower color dark red and yellowish brown are independent monogenic dominants to light yellow; dark red is epistatic to yellowish brown.   The spontaneous appearance of a female plant with stamens aborted is again recorded by Blaringhem.

Chelidonium majus L.   (Dahlgren, *104;* Heijl and Littien, *196;* Sax, *467;* De Vries, *528, 529, 530*.)

Doubleness is recessive to singleness, but several degrees of doubling appear in F_2.   The laciniate leaf type and the "minus" leaf type are independent monogenic recessives to the normal leaf type.

Chrysanthemum.   (Miyake and Imai, *362;* Shimotomai, *470;* De Vries, *528*.)

De Vries found yellow flower color dominant to white in *Chrysanthemum roxburghi*.   A hybrid, *C. marginatum* (90 chromosomes) $\times$ *C. morifolium* (54 chromosomes), is highly fertile and appears to be established as a constant 144-chromosome type; *C. decaisneanum* (74 chromosomes) $\times$ *C. indicum* (36 chromosomes) produced a sterile hybrid.   A clone with flowers variegated white and magenta, which occasionally produces pure white flowers, is shown to be a chimera.

Clarkia elegans Douglas.   (Bateson, *17;* Rasmuson, *432*.)

Four genes for color are recognized; the order of dominance is purplish red, salmon red, light red, and white.

Clarkia pulchella Pursh.   (Rasmuson, *432;* De Vries, *528, 530*.)

Three genes for color are recognized; purple is dominant to purplish red; completely colored flowers are dominant to colored with white margins, and colored flowers dominant to white.

Clitoria ternatea L. (Rant, *424*.)

Blue flowers are dominant to white; peloric flowers to nonpeloric.

Coleus. (Correns, *102*.)

A variegated form of *Coleus hybridus*, "albopicta", is influenced by environment, but probably is inherited as a dominant.

Collinsia. (Hiorth, *207, 209, 210, 211;* Rasmuson, *431*.)

Hiorth found white-spotted leaves, red-nerved leaves, and white flowers to be linked in *Collinsia bicolor*. Later he reported a study of 12 genes in this species, which fall into five or more linkage groups. The cross *C. bicolor* × *C. bartsiae-folia* produced a nearly sterile F_1, which was further almost sterile on backcrossing to either parent. Various backcrosses and F_2 and F_3 generations were nevertheless produced. Two partly fertile tetraploids, larger than the diploids, were extracted, one from an F_2 progeny and one from the progeny derived from selfing a backcross plant. Rasmuson reports two complementary genes for flower color in *C. bicolor;* one of these independently produces a red tinge in the stems, which is dilute in heterozygous condition. He also finds that the occurrence of spots on the upper lip of the flower in *C. tinctoria* is a monogenic dominant to the lack of spots. Yellow variegated plants in this species are simple recessives to normal.

Coreopsis tinctoria Nutt. (De Vries, *528*.)

Yellow flowers are dominant to brown (var. *brunnea*).

Cosmos bipinnatus Cav. (Miyake, Imai, and Tabuchi, *363, 364*.)

A gene for full coloration and a gene for crimson, each acting only in the presence of a basic gene for color production, are postulated to explain the flower color classes crimson, pink, shaded, and white. Basal blotch on the ligulate flowers is considered to be a monogenic dominant to absence of the blotch. The character "double ring" of color on corollas is determined by two complementary genes. The inheritance of pollen color and an abnormal flower type, "bracteoid", have also been studied. Linkage between two genes has been established.

Cypripedium (and *Paphiopedilum*). (Hurst, *220, 222, 223, 224*.)

Rose purple color is conditioned by two complementary genes; hence certain pairs of albinos yield colored offspring on crossing. A third gene produces dilution of color when recessive.

Dahlia variabilis Desf. (Lawrence, *310, 311, 312*.)

The dahlia has been shown to be an octoploid, having eight times the haploid number of chromosomes, i. e., a gene or its allelomorph may be represented from one to eight times in a given individual. The yellow and ivory flower colors are both dominant to white, yellow showing tetrasomic inheritance, and ivory, disomic inheritance. Magenta, purple, orange, scarlet, and crimson flower colors are the result of anthocyanin pigments showing over yellow and ivory flavone ground colors. Anthocyanin color apparently shows tetrasomic inheritance. Ivory and yellow flavone colors come from different ancestors, and the chromosomes bearing them do not pair. Similarly the two anthocyanin color genes occur in two different quadrivalent sets of chromosomes. Lawrence has also studied inheritance of a recessive albino flower type which is unstable, producing frequent somatic variation.

Delphinium ajacis L. (Demerec, *110*.)

Demerec studied inheritance of two unstable (mutable) genes, rosa-alpha and lavender-alpha, which frequently revert to their normal allels.

Delphinium orientale Lose. (Beckman, *43*.)

One dwarf type (nana) is a simple monogenic recessive to normal. A second dwarf (nanella) is also recessive, but shows irregular segregation. Double flowers are monogenically recessive to single. The abnormal "ranuncula-flower" type of double is dominant to the common double. Five genes for color are postulated to explain the inheritance of corolla color. The wild color (red-violet) is dominant over all other colors. A case of linkage is reported.

Dendrobium. (Hurst, *223, 224*.)

Purple flower color is dependent on two complementary genes. Certain albinos yield colored forms on crossing.

Dianthus barbatus L. (Lilienfeld, *324, 325*.)

In some varieties the flower color may change during the lifetime of the flower. When crossed with normal types this condition was found to be dominant. Singles × doubles give singles in F_1, and a ratio of 3 singles to 1 double in F_2. Normal growth is also a monogenic dominant to dwarf. At present three linkage groups have been established.

Dianthus caryophyllus L.   (Batchelor, *15;* Connors, *81;* Saunders, *458.*)
    White flowers are dominant to yellow, and red yellow flowers to red.   A
monogenic difference exists between the bullhead type (extremely double) and
the single type; the commercial standard double is the heterozygous form.
Digitalis gloxiniaeflora Hort.   (Warren, *534.*)
    Nonpeloric is dominant to peloric, purple to white corolla color, and purple
spotting on the corolla to brown spotting.
Digitalis purpurea L.   (Haase-Bessell, *158, 159;* Keeble, Pellew, and Jones, *290;*
Miyake and Imai, *350;* Saunders, *452, 459;* Shull, *475.*)
    Conflicting reports exist as to inheritance of some characters.   These may be
due to differences in the actual varieties studied.   White flower color has been
reported both as a dominant and as a recessive.   Some foxglove plants have the
topmost flower of a distinctly different type, which is called peloric.   This
condition is reported as a simple monogenic recessive to normal.   It is also
reported as very complex in inheritance.
Digitalis species hybrids.   Buxton and Dark, *65;* Buxton and Darlington, *66,
67;* Hill, *205;* Michaelis, *346.*)
    According to Hill, reciprocal F_1 hybrids of *Digitalis purpurea* and *D. lutea*
are unlike, and in each case the hybrid resembles the maternal parent in size
of calyx and corolla.   Michaelis also found the F_1 progeny from *D. purpurea*
(56 chromosomes) $\times$ *D. lutea* (96 chromosomes) unlike the reciprocal.   The
F_1 chromosome number was 76 in the somatic cells.   *D. mertonensis* (112
chromosomes), a fertile tetraploid giant, arose from a cross of the two diploid
species *D. purpurea* and *D. ambigua* (56 chromosomes in each).   It forms only
sterile hybrids with other species, both diploid and tetraploid.   Various hybrid
combinations of diploid species are also sterile.
Dolichos lablab L.   (Harland, *194.*)
    The climbing habit behaves as a monogenic dominant to the bush habit.
Flower color, seed-coat color, and plant color are closely correlated.   In the
F_2 of a cross between two white-flowered varieties, flower color segregated 9
purple: 7 white, and one of the white classes showed intermediate seed and stem
coloration.   Two genes are assumed: one determines purplish-brown seed coat
and purplish hairs on the stipules, the other is epistatic to the first and produces,
together with it, purple flowers, black seed, and colored nodes.
Dracocephalum thyrmiflorum L.   (Dahlgren, *107.*)
    The variety *pallida* (with white flowers, green plants) is a monogenic recessive
to the *typica* form (with blue flowers and anthocyanin in the plant).
Epilobium angustifolium L.   (Correns, *82, 83.*)
    The white-flowered variety is a monogenic recessive to the red-flowered type.
Epilobium hirsutum L.   (Przyborowski, *413;* Stomps, *495.*)
    An abnormal type, "cruciata", is a monogenic recessive to normal.   A
monogenic difference was found between two types of spines on pollen grains.
Epilobium species hybrids.   (Lehmann, *319, 320, 321;* Lehmann and Schwemmle,
322; Michaelis, *345, 347, 348, 349.*)
    Hybrids of most species of *Epilobium* other than *Epilobium parviflorum* and
E. hirsutum are reciprocally alike, but crosses involving the species mentioned
yield reciprocally unlike hybrids.   Differences between the reciprocals are found
in size of organs, including flower size, in pollen fertility, and in reaction to
mildew.   The role of cytoplasmic inheritance in these differences has been
intensively studied.   A giant form twice the normal size but with a diploid
complement is described (*322*).
Eschscholtzia mexicana Greene.   (Uphof, *525.*)
    White flower color is a monogenic dominant to yellow, and white to orange.
Orange self-color is dominant to orange base on yellow petals.
Euphorbia pulcherrima Willd.   (Robinson and Darrow, *439.*)
    The pink form of the poinsettia is a chimeral sport from the red.   White is
apparently a mutation from red.
Freesia.   (Morgan, *376.*)
    Several unusual types appearing from spontaneous hybridization are de-
scribed.
Galeopsis.   (Hammarlund, *193;* Müntzing, *380, 381, 382, 383, 384.*)
    In *Galeopsis tetrahit*, immunity to mildew (*Erysiphe labiatanum*) is a mono-
genic recessive to susceptibility; heterozygous forms show partial resistance.
Müntzing has studied crossability, cytology, and genetics of species and 80
biotypes.   Three groups of species do not intercross: *Ladanum, pubescens-*

speciosa, tetrahit-bifida. Five species hybrids within the subgenus *Ladanum* were produced. A triploid that appeared in the F$_2$ of a cross *G. pubescens* $\times$ *speciosa* gave rise to a tetraploid on crossing with *G. pubescens* as pollen parent. This tetraploid agrees closely with *G. tetrahit* in appearance and in cytological and breeding behavior. Spontaneous *G. tetrahit* is believed to have arisen from the above species in a similar manner. On intercrossing pure lines of *G. tetrahit*, 14 combinations gave high fertility in F$_1$, and 6 showed partial sterility. Partial sterility is attributed to a lethal gene, which destroys all pollen grains, but only part of the ovules containing it. In *G. tetrahit* and *G. bifida*, inheritance of flower and stem color and rate of sterility have also been analyzed genetically.

Gardenia florida L. (Capimpin, *68.*)
Incomplete data on inheritance of doubleness and fertility were obtained.

Geranium robertianum L. (Dahlgren, *107.*)
White flower color, "leucanthum", is a monogenic recessive to red.

Geum. (Dahlgren, *107;* Marsden-Jones, *333;* Rosén, *443;* Weiss and Rosén, *539.*)
The inheritance of certain characters has been studied in hybrids involving *Geum* species. The presence of anthocyanin is a monogenic dominant to its absence. Large flowers were dominant to small and the F$_2$ segregation indicated the presence of several genes. Yellow was a monogenic dominant to nonyellow, and red was dominant to nonred. The experimental hybrid *Geum urbanum* $\times$ *G. rivale* is indistinguishable from the naturally occurring *G. intermedium;* the reciprocal cross was not successful. Inheritance in *G. intermedium* is often irregular.

Godetia amoena Lilja. (Rasmuson *429, 433.*)
Each of two types of petal spots, on crossing with unspotted *Godetia whitneyi*, proved a monogenic dominant to the unspotted condition. When intercrossed the F$_1$ showed both types of spot; in F$_2$, 1 "basal fleck" : 2 double spot : 1 "querfleck" appeared. Rasmuson suggests the two genes are closely linked. Double flowers are dominant to single, but degree of doubleness is influenced by the petal-spot genes mentioned above.

Godetia whitneyi T. Moore. (Rasmuson, *429, 433.*)
Crosses involving different flower colors showed the following monogenic dominants: White over yellow-margined white, red over lilac, rose lilac over lilac, red-spotted over lilac, red over red-spotted, large spot over small spot, and light-margined red over pure red. Single flowers are more or less completely dominant over double ones.

Helichrysum bracteatum Andr. (Dambekalns, *109.*)
Three genes affecting white and yellow involucre color are established. Sulphur and orange are simple dominants to recessive white; the two dominants together condition gold. The third gene, dominant white, inhibits expression of sulphur, orange, and gold.

Hibiscus rosa-sinensis L. (Mendiola, *342, 343.*)
Lobing of seedling leaves was found to be a monogenic dominant to entire leaves. Self-sterility appeared to be correlated with absence of lobing. Single flowers appearing on normally double plants were self-sterile; on crossing with normal singles they bred like doubles. The occurrence of flower color sports is recorded.

Hibiscus sabdariffa L. (Howard and Howard, *218.*)
Eight genes are assumed for color in corolla, calyx, pollen, stem, and leaves. One gene may affect several parts of the plant, e. g., a gene for red in corolla eye, pollen, leaves, and stem is a monogenic dominant to its absence.

Hyacinthus. (De Mol, *372.*)
Hyacinth bulbs X-rayed during flower formation may show somatic variations in flower, leaf, or pollen characters. Somatic variation in flower color on a single flower stalk may be the result of mutations induced by changes in environmental conditions during flower formation.

Impatiens balsamina L. (Bedell, *44;* Hagiwara, *177;* Kanna, *280, 281, 284, 285;* Rasmuson, *425, 432.*)
At least three genes for flower color are known. White is recessive to blue-red, and to blue. A dominant gene for intensification of flower color is also reported. In color patterns, white flecking on colored flowers is reported by one investigator as a simple dominant to nonflecking; another reported it as a recessive. There are two types of double flowers, the common and the "camellia", which latter is correlated with a dwarfish stature. Single is a monogenic

dominant to common double; but the cross single × camellia gave in F_2, 9 single: 3 common double: 4 camellia double.   In a recent study (by Kanna) 16 genes are recognized, 3 lying in each of 2 linkage groups, the others showing largely independent inheritance.   Ten genes are concerned with flower color, 3 with flower type.   Winged flowers, peloric double flowers, and 3 defective types—"white blotched", "deficient", and "fasciated"—are all simple recessives to normal. A nonheritable type of fasciation also occurs.   Striped flowers are determined by a mutable gene.

Ipomoea hederacea Jacq. (*Pharbitis nil*).   (Hagiwara, *161, 162, 163, 164, 165, 166, 167, 168, 169, 170, 171, 172, 173, 174, 175, 176, 178, 179, 180, 181, 182, 183, 184, 185, 186, 187, 188, 189;* Imai, *233, 234, 235, 236, 237, 238, 239, 240, 241, 242, 243, 244, 245, 246, 247, 248, 249, 250, 251, 252, 253, 254, 255, 256, 257, 258, 259, 260, 261, 262, 263, 264, 265, 266, 267;* Imai and Kanna, *268, 269;* Imai and Tabuchi, *270, 271, 272;* Miyake and Imai, *351, 354, 358, 359, 360, 361;* Miyazawa, *365, 366, 367, 369, 370, 371;* Sô and Nishimura, *490;* U, *520;* Yamaguchi, *556, 557;* Yasui, *562, 563*.)

In the Japanese morning-glory white flower is a monogenic dominant to colored.   At least six different white types exist.   Some white × white crosses give colored in F_1, and a 9 : 7 ratio of colored to white in F_2.   A complex interaction of complementary genes gives various white types in combination with a variety of different colored tubes, stems, and seeds.   Genes modifying color have also been studied.   The color of the inside of the tube seems to be controlled by a complex interaction of genes.   The inheritance of various types of corollas has been studied, and the action of complementary and inhibiting genes reported.   Five abnormal flower types were all monogenic recessives to the normal.   Five types of doubleness have also been found to be simple recessives to normal.   At least 17 abnormal leaf types are also simple recessives to normal.   The literature of *Ipomoea* (*Pharbitis*) is more extensive than that of any other plant discussed here, due to intensive studies of a number of Japanese workers with fundamental objectives.   Summary papers now appearing indicate that cultivated forms have arisen mainly through recessive mutations from the prototype; of the 111 genes described, only 15 are dominant; 70 genes have been located in 12 linkage groups (there are 15 pairs of chromosomes); 21 genes are concerned with flower color; 20 genes affect form of the leaf; 10 chlorophyll defects showing genic inheritance and 4 showing plastid inheritance are recognized; 20 genes of low stability (mutable genes) have been described; a provisional map of 1 chromosome showing linkage intensity, and many calculations of crossing over between specific gene pairs have appeared.

Ipomoea imperialis.   (Correns, *98*.)

Two chlorophyll deficiencies, "chlorina" (pale green) and "albomarmorata" (white spotted), proved to be independent recessives to normal green.

Ipomoea purpurea (L.) Roth.   (Barker, *12;* Imai, *234, 247*.)

Inheritance of flower color is controlled by interaction of several genes. Flaking of petals is a dominant character.   Flower color and stem color are intimately related.   Flower doubleness was found to be a monogenic dominant over singleness.

Iris.   (Bliss, *53:* Colin and Carles, *78;* Reed, *435;* Simonet, *479*.)

Observations on color in bearded iris show Mendelian inheritance of brown-tipped beard, and colored leaf bases.   Simonet reports four species-hybrids not yet of flowering size.   Colin and Carles find that only species having the same glucosidal reserve can be crossed.   Reed has described an F_2 population of a cross between *Iris fulva* and *I. foliosa*, obtained by selfing the garden variety Dorothea K. Williamson, a hybrid between these two species.   The F_2 progeny showed a great range of color including types with pure yellow flowers.

Lamium.   (Correns, *101;* Müntzing, *378, 385;* Sirks, *482, 485*.)

A peloric flowered form of *Lamium album* was recessive to the normal, but the F_2 ratio indicated five or more genes were involved.   Another type with protruding stamens was also recessive, differing from normal by four or more genes.   Yellow pollen in *L. hybridum* proved to be a monogenic recessive to red pollen.   A type with the lower lips of the flower reduced behaved as a monogenic recessive to normal in *L. maculatum*.   A cleistogamous flower type in *L. amplexicaule* showed a simple factor difference from open-flowered, with no dominance.   In some species the summer annual habit (surviving only by seed) and the winter annual habit (surviving vegetatively) are modifiable; in *L. purpureum* an obligate winter annual type was found to differ geno-

typically from the facultative winter annual. Inheritance of flower color, time of bloom, height, and vigor were also studied.

Lathyrus odoratus L. (Bateson, *17;* Bateson and Punnett, *20, 21, 22;* Bateson and Saunders, *23;* Bateson, Saunders, and Punnett, *24;* Bateson, Saunders, Punnett, and Hurst, *25;* Gregory, *146;* Punnett, *414, 415, 416, 418, 419, 420;* Stone, *496;* Thoday and Thoday, *508.*)

In flower color the following mongenic differences were found, dominant genes being given first: White v. cream, colored v. white, purple v. red, bright v. dull color, full v. dilute color, light v. dark wings, purple v. copper, purple v. maroon. Two identical appearing whites give a purple F_1, and nine purple to seven whites in F_2. A gene for bright color, one for full color, one for light wings, and one for purple act as modifiers for both purples and reds. Other color patterns, as marbling and flaking, are either recessive or heterozygous and not fixable. The four types of growth habit are tall, bush, cupid, and bush-cupid. Cupid × bush gives the normal tall. A form with sterile anthers is a simple recessive to normal. Punnett summarized the data on inheritance in sweet pea in 1924. More recently (1932) he has described five linkage groups and two unassigned genes in *Lathyrus*, corresponding to the seven pairs of chromosomes. Stone reported a somatic mutation from the cupid type to normal tall.

Lilium. (Griffiths, *151;* Heinricher, *198;* Preston, *410.*)

In a cross *Lilium* sp. × *L. croceum,* presence of bulbils was recessive to their absence. In F_2 segregation, parental and hybrid types appeared. In *L. bulbiferum* × *L.* sp. (*tigrinum ?*), bulbils again proved recessive. Griffiths and Preston have listed successful species-crosses.

Linaria. (Correns, *91, 95;* East, *116;* Saunders, *453;* Sirks, *484.*)

Pink flower color in *Linaria* is recessive to blue; orange color in the palate is recessive to its absence. Red × white-flowered *L. moroccana* yielded blue in F_1; in F_2, nine blue : three red : four white. Orange color in the palate is dominant to its absence in *L. vulgaris.* Data on inheritance of sterility collected by Correns have been explained by Sirks according to the scheme applied to *Nicotiana, Veronica,* etc. East reports cross-compatibility of 18 species or varieties of *Linaria.* Purple flowers are dominant to white, and trailing habit to bushy, in *L. cymbalaria.* Copper-colored flecks in the corolla are dominant to nonflecked in *L. broussonnetti* × *perezi.* Four genes are concerned in development of flower color in crosses of *L. sapphirina, L. moroccana,* and *L. reticulata.*

Linum species other than *L. usitatissimum.* (Correns, *99;* Hobusch, *212;* Laibach, *307, 308;* Tammes, *503.*)

In *Linum perenne* and *L. austriacum* the long-styled type is a monogenic recessive; the short-styled type is heterozygous. Self-fertility is apparently dominant to self-sterility. Several grades of self-fertility occur. In *L. austriacum* the difference between long and short style appears to be governed by more than one gene. Tammes has summarized the genetics of *Linum* up to 1928. Hobusch was able to grow the F_1 of *L. austriacum* × *L. perenne* by culturing the normally nonviable seeds on artificial media while still immature. Studies of backcrosses and later generations indicated that the proportion of good seeds is determined by degree of relationship of the parent lines.

Lobelia. (Saunders, *465.*)

An extensive series of flower types from singles through semidoubles to full doubles with five perianth whorls and no stamens occurs in *Lobelia.* Full doubles are sterile, singles are pure-breeding, but genic analysis of semidoubles is not complete.

Lunaria annua L. (Correns, *89.*)

The white-margined leaf type, "albomarginata", is a mongenic recessive to normal.

Lupinus angustifolius L. (Fruwirth, *138;* Hallqvist, *192;* Kajanus, *276;* Roemer, *440, 441;* Sypniewski, *502;* Vestergaard, *526, 527.*)

In flower color, monogenic differences were found between blue and white, blue and red, and red and white. Some crosses between red and white, however, gave a blue F_1, and nine blues : three reds : four whites in F_2.

Lupinus species other than *L. angustifolius.* (Burlingame, *63;* Kajanus, *276; 277.*)

In *Lupinus luteus* the black-seeded type is a monogenic dominant to gray. In *L. mutabilis* blue flowers proved monogenically dominant to white. Work-

ing with *L. apricus* var. *vallicola, L. pipersmithi,* and *L. nanus,* Burlingame found a white-striped flower type, which segregated into dark blue, white-striped, and white. This was interpreted on a single gene basis, the white striped being the heterozygous type. Light-blue flowers were mongenically dominant to dark-blue. Dark seeds are associated with dark-blue flowers but probably not determined by the same gene.

Lychnis (including *Melandrium* and *Viscaria*). (Åkerlund, *2;* Bateson and Saunders, *23;* Baur, *30;* Correns, *85;* Shull, *473, 474, 476, 477, 478;* Tjebbes, *512;* De Vries, *528 530;* Winge, *548, 549.*)

Lychnis species are normally dioecious, having the male and female flowers on separate plants. Much of the genetic literature concerns the technical problem of sex inheritance. Constant-breeding hermaphrodites are maintained by a system of balanced lethals. Purple flowers are dominant to white. Broad leaf is a monogenic dominant to narrow leaf; it is also apparently sex-linked. Chlorophyll deficient types are recessive to normal green. Winge (*549*) reports that "aurea", a chlorophyll defective, is a sex-linked recessive, restricted to male plants because it is lethal where homozygous. "Variegated", another chlorophyll defect, is limited to female plants. Åkerlund found *Melandrium album* more winter hardy than *M. rubrum,* the F_1 intermediate. Back-crosses to *M. album* were more hardy when the hybrid was the pollen parent than in the reciprocal backcross. Tjebbes recognized four recessive types—"broom growth", "rolled corolla", "transparent corolla", and "biennial type", isolated from inbreeding garden strains of *Viscaria* (*Lychnis*).

Lythrum salicaria L. (Barlow, *13, 14;* East, *112, 113, 114, 115;* Ubisch, *521, 523.*)

The styles of this species occur in three different length classes. Genetic investigation has been largely concerned with inheritance of style length. A two-factor hypothesis failed to account for certain midstyle types, and a balanced lethal hypothesis at present seems most tenable (East, *115*).

Malope trifida Cav. (Rasmuson, *426.*)

A white-flowered type proved to be a monogenic recessive to red-flowered.

Matthiola incana (L.) R. Br. (Bateson and Saunders, *23, 24, 25;* Correns, *83;* Fisher, *130;* Frost, *134, 135, 136, 137;* Goldschmidt, *144;* Kappert, *286;* Lesley and Frost, *323;* Muller, *386;* Philp and Huskins, *408;* Saunders, *451, 454, 455, 456, 457, 460, 461, 463, 464;* Snow, *488, 489;* Tschermak, *518, 519;* Waddington, *531;* Winge, *550.*)

A cross of rose × white gave a purple F_1 and a trigenic segregation of 27 pale purple : 9 deep purple : 9 rose : 3 deep red : 16 white in F_2. There are also genes that dilute the colors. Two genes are necessary for the production of anthocyanin; if one or both are absent, the flower is uncolored. There is also a gene converting all reds to purple, and another causing the difference between the pure and dull color. Cream is due to pigment in the plastids. It behaves as a monogenic recessive to white. Doubleness is recessive to singleness (for discussion of this question, see section on double-flowering stock). Earliness in blooming is dominant to lateness as is open growth habit to compactness. Saunders has summarized the published data on breeding of stocks to 1928.

Meconopsis cambrica Vig. (Saunders, *458.*)

Doubleness is dominant to singleness, a single gene being involved.

Mimulus. (Brožek, *56, 57, 58, 59, 60, 61, 62.*)

Inheritance of several characters in *Mimulus quinquevulnerus, M. tigrinus,* and *M. tigrinoides* has been studied. Distribution of color spots over the entire petal surface behaves as a monogenic dominant to spots limited to half the surface. Single flowers are dominant to doubles, two genes being able to inhibit the double condition entirely or partly. Plants with a terminal flower differing from lower flowers showed dominance of this character. Two genes concerned in flower color have been established in *M. cardinalis.* One determines development of yellow plastids, the other anthocyanin sap color.

Mirabilis jalapa L. (Baur, *28;* Correns, *84, 85, 88, 89, 90, 92, 93, 94, 96;* Kanna, *283;* Kiernan and White, *299;* Marryat, *332;* Showalter, *471, 472.*)

Flower color inheritance in *Mirabilis* shows many cases of intermediate hybrids that cannot be made pure. White × yellow gives pale yellow in F_1 and one white : two pale yellow : one yellow in F_2. White × crimson gives deep magenta, and yellow × crimson, orange red, in a 1:2:1 F_2 ratio in each case. White × crimson, and white × yellow both give magenta rose in F_1, and a very complex F_2. White × white gave white F_1 and F_2. In one instance two whites

gave colored F_1 types. The striped varieties are all heterozygous, segregating to self colors and striped in F_2. In other characters tall is dominant to half dwarf and to dwarf. Half dwarf is dominant to dwarf. Kanna and Showalter independently interpret flower color expression on the basis of two series of multiple allels, one series governing base color, the other modifying color expression. Mutable genes are found in each series. Showalter describes a mutant growth type, "box", which is a monogenic recessive.

Myosotis. (Chittenden, *71.*)
Two genes for flower color are assumed. Pink is dominant to white and blue is dominant to pink.

Nemesia strumosa Benth. (Riley, *438.*)
At least four intrasterile, interfertile lines occur in this self-sterile species.

Nemophila atomaria Fisch. and Mey. (Chittenden, *70.*) ·
Three genes are postulated to explain inheritance of flower color (lilac, black, red, pale brown) and four other genes for inheritance of color distribution. Apparently lilac is dominant to black, black to red, and red to pale brown. The spotted flower coloration is a monogenic dominant to full-colored.

Nemophila insignis Brand. (Chittenden, *70.*)
Blue flower color is dominant to mauve and to white. Mauve × white produced blue flowers in F_1.

Nemophila liniflora Fisch. and Mey. (Chittenden, *70.*)
At least three genes for flower color and color distribution are assumed. Pale-blue flower color is a simple dominant to purplish blue, and spotted eye (spotted with black) is dominant to full black eye, the two genes showing independent inheritance. One or two basic genes for flower color are also postulated. Black spotted leaves are determined by a single gene, the recessive condition being white spotted leaves.

Nigella damascena L. (Toxopéus, *514.*)
Long stems are dominant to the dwarf form. Crosses between yellow variegated and green plants give green in F_1, and 3 green to 1 yellow variegated in F_2. Single flower was a simple monogenic dominant to normal double. A second double type was dominant to single, and in F_2 no single plants appeared. In studies of color inheritance, colored was dominant to ivory white, blue to violet, and dark blue to pure white.

Nymphaea. (Anonymous, *1.*)
A dominant white is reported.

Odontoglossum. (Hurst, *222.*)
Blotched flower is dominant to self-colored, and yellow-flowered to white.

Orchidaceae. (Colman, *79;* Godfrey, *142.*)
Two lists of successful orchid hybrids, including intergenic hybrids, have appeared.

Oxalis corniculata L. (Nohara, *394.*)
Purple in leaves and in the eye of the flower is monogenically dominant to its absence.

Oxalis rosea Jacq. (Ubisch, *522, 523, 524.*)
Two genes for flower color are recognized, one producing light rose when present in the dominant form, and with a second gene, rose color; white is the recessive. Three genes for style length are assumed; each of the two genes for flower color shows linkage with one of these.

Oxalis valdiviana Hort. (Barlow, *13, 14;* Ubisch, *524.*)
The mechanism of inheritance of style length is, according to Ubisch, similar to that in *Oxalis rosea.*

Paeonia. (Saunders, *449.*)
Twenty-nine hybrid strains have flowered. An F_2 population from the cross *Paeonia albiflora* × *macrophylla* has matured. Two abnormal strains and a few types of ornamental value have appeared.

Papaver rhoeas L. (Becker, *42;* Negodi, *387;* Newton, *389;* Philp, *406, 407;* Rasmuson, *430;* Shull, *476.*)
A white margin of the petals is dominant to its absence. Seven genes for flower color have been isolated and belong in three linkage groups. Nine genes are established by Philp (*407*). Doubleness is determined by several genes. Albinism is a simple recessive to normal, and is independent of flower color. In hybrids of *Papaver rhoeas* and *P. commutatum* the characters of the latter species are largely dominant.

Papaver somniferum L. (De Vries, *528, 530;* Fruwirth, *139;* Hurst, *221*; Ishikara, Kobetsu, and Kojima, *273;* Kajanus, *278, 279;* Kasaeva, *287;* Leake and Prasad, *313, 314;* Miyake and Imai, *353, 355, 356.*)

The basal spot on petals is dominant over its absence. Color in the petal is dominant over white, and purple is dominant over red. When flowers are heterozygous for color genes they usually produce progenies with considerable variations in intensity of color. Other color genes have been studied. In plant size, large is a simple dominant over small, and nonstriped petals over striped. Other simple dominants are single over double flowers, and laciniated over entire petals. The cross *Papaver somniferum* × *bracteatum* was successful; the reciprocal produced no viable seeds. The F_1 plants were perennial, very variable, including some monstrous forms. F_2 plants were obtained.

Pelargonium zonale Willd. (Ballard, *9;* Baur, *30;* Moncrieff, *373;* Noack, *392, 393;* Roth, *445.*)

Inheritance of doubleness is incompletely analyzed, singleness is regarded as dominant. A golden-leaved type, "aurea", is a heterozygous form, segregating on selfing into 1 normal green: 2 "aurea": 1 pure yellow. The pure yellow dies in the seedling stage or earlier. The "freak of nature" variety, the leaves of which have white centers and green borders, is not a chimeral type. This leaf character is inherited through both egg and pollen. The chemical nature of dominant rose-pink and recessive salmon-pink flower colors, and of other colors, is interpreted by Moncrieff.

Petunia violacea Lindl. (Ferguson, *126, 127;* Frost, *134;* Harland and Atteck, *195;* Kostoff and Kendall, *302;* Malinowski, *328, 329, 330;* Malinowski and Skalińska, *331;* Matuda, *340;* Moore and Haskins, *375;* Rasmuson, *428;* Sachs-Skalińska, *446, 486;* Saunders, *450, 456;* Savelli, *466;* Terao, *504;* Terao and Nagaharu, *505;* Terao and U, *506;* Tjebbes, *510, 511;* Ubisch, *522;* West-gate, *540;* Yasuda, *559, 560.*)

Color inheritance was mostly simple monogenic with violet dominant over red, also over lilac. Uniform coloring is dominant over green-edged flowers. Violet red × white gave an intermediate F_1, and a 1:2:1 ratio in F_2. Other colors were more complex. Doubleness exists in a wide range of degree. It is caused by stamens becoming petals. Singles × singles give all singles. Singles × doubles give a 1:1 ratio. Doubles × doubles give about 3 doubles to 1 single. In *Petunia axillaris* and *P. violacea*, the progenitors of the cultivated petunias, four pairs of genes determine pollen color. The white flower color of *P. axillaris* was inherited as a recessive in a cross with a royal purple garden form, but the parental purple was not recovered in F_2. Both *P. axillaris* and *P. violacea* are usually self-sterile, and the F_1 is only partly fertile. Garden forms are sometimes fertile, but several grades of self-sterility also occur. Harland and Atteck (*183*) interpret self-sterility on the basis of four multiple allels. By bud pollination they were able to self four normally self-sterile lines, finding one homozygous lethal, one dwarfed, the other two normal in appearance. One or more variegated types show irregular inheritance. Mutations have been induced by X-ray treatment of seed and of flower buds. Some garden petunias are tetraploid, showing irregular behavior on crossing with diploid varieties. Petunia pollen has been shown to stimulate fruit formation in eggplant (*Solanum melongena*), but no seeds are formed.

Phacelia. (Chittenden, *70.*)

Two species, *Phacelia parryi* and *P. whitlavia* were found to cross readily and furnish fertile offspring. Purple flowers proved dominant to bicolored (purple limb and white tube), and bicolored dominant to white. A recessive giant type was found in *P. parryi*, and a recessive entire-leaved form in *P. whitlavia* var. *alba*.

Phlox drummondii Hook. (Flory, *132;* Gilbert, *141;* Kelly, *291, 292, 293, 294, 295, 296, 297;* Kelly and Wahl, *298.*)

Five genes are assumed to account for the inheritance of flower color by Gilbert (*141*). Kelly interprets flower color according to a seven-gene scheme. Cream-yellow is a monogenic recessive to white. A semidouble type is apparently influenced by more than one gene. Salver-shaped corolla is monogenically dominant to funnel-shaped. Entire petals are due to one gene; the recessive form is deeply cut, and the heterozygous form is the "fimbriata" type. Style-lessness and fasciation are each monogenic recessives to normal. Attempts to cross *Phlox paniculata* with *P. drummondii* yielded infertile F_1 progeny; *P. divaricata* × *drummondii* produced an F_1 that developed a few seeds (*132*).

Polemonium. (Correns, *86;* Dahlgren, *104, 106;* Ostenfeld, *399, 400, 401;* De Vries, *528, 530.*)

Blue corolla color in *Polemonium caeruleum* is monogenically dominant to white, pinnate leaf form to bipinnate, normal petal to small narrow petals, and normal green leaves to the pale green (chlorina) type. Both the blue and the white flower colors of *P. caeruleum* proved dominant to the yellow of *P. flavum* in F_1, but these interspecific hybrids were sterile. *P. mexicanum* × *pauciflorum* yielded intermediate forms in F_1, with complex segregation in F_2 and later generations, most of the segregates proving fertile. The reciprocal cross yielded no seed, possibly because *P. pauciflorum* styles are eight times as long as those of *P. mexicanum.* Crosses of *P. caeruleum* with *P. carneum* and with *P. filicinum* yielded only sterile plants in F_1.

Portulaca grandiflora Hook. (Blakeslee, *47;* Blakeslee and Avery, *49;* Enomoto, *118, 119;* Ikeno, *228, 229, 231, 232;* Okura, *398;* Tjebbes, *509;* Yasui, *561.*)

Color of floral parts and vegetative parts are correlated with each other. The interaction of five genes for color has been studied. One special white race is a dominant white with a recessive lethal effect. Pure whites of this type are not produced. When selfed it gives two special whites to one normal white. About one-fourth of the seeds from selfing special white are nonviable. Mosaics on the corolla are heterozygous. A Mendelian analysis has not been made. Doubleness is a simple dominant to singleness. Dwarf type is a simple recessive to normal. This gene reverts to normal fairly frequently. Dwarf plants bear normal branches, and vice versa. Ikeno reported that inheritance of purple-spotted flowers did not conform to Mendelian theory. The species is normally self-fertile, but Tjebbes found a self-sterile variety within which two self-sterile but cross-fertile groups occurred. Okura identified as haploids three dwarf individuals from F_2 and F_3 generations of a cross. These produced an occasional normal diploid on being pollinated with normal pollen.

Potentilla. (Müntzing, *379.*)

Constancy of biotypes within several species of *Potentilla* is due to perfect pseudogamous maternal inheritance. Pollen is not functional, but pollination of emasculated flowers is necessary for setting of seed.

Primula. (Altenburg, *3;* Bateson and Gregory, *19;* Buxton, *64;* Chattaway and Snow, *69;* Chittenden, *70;* Correns, *102;* Dahlgren, *103; 108;* Ernst, *121, 122, 123;* Frimmel, *133;* Gregory, *147, 148, 149;* Gregory, De Winton, and Bateson, *150;* Heinricher, *199;* Huskins, *227;* Keeble and Pellew, *288, 289;* Marsden-Jones and Turrill, *337;* Pellew and Durham, *405;* Raunkiaer, *434;* Sansome, 447; Sömme, *491;* Ubisch, *523;* De Winton, *551, 552, 553, 554;* De Winton and Haldane, *553;* Zollikofer, *564.*)

According to Frimmel (*133*), three pigments occur in flower colors of the garden primrose—anthocyanin, carotin, and anthochlor yellow; 260 color tones are recognizable. Carotin inheritance is monogenic, anthocyanin is digenic, with a factor for red and another for blue, the two together developing a blue-violet; white is recessive. Colors approaching black result from association of the gene for carotin with the two anthocyanin genes. Heterozygotes are expressed as various color tones. Four forms of the "eye" of the flower in *Primula sinensis* are known. Small eye is a monogenic dominant to large eye, and white eye acts in varying degrees as dominant over both small and large eyes. A fourth type, large greenish eye, is a monogenic recessive to normal. Two types of doubleness occur. Each is a monogenic recessive to normal. In several species of *Primula* normal forms have short styles with anthers borne above the stigma, or long styles with anthers at a lower level. These are self-sterile. Crossover types with long styles and anthers at the higher level and short styles with anthers at the lower level are infrequent but self-fertile. The short-style type is a simple dominant to long-style, except in *P. hortensis,* in which two genes are assumed. In *P. obconica* fertility is lower when forms of like style length are crossed than when unlike lengths are crossed. In *P. hortensis* and *P. acaulis* fertilization of normally incompatible forms was accomplished by pollinating stubs after removal of styles. In crosses of *P. juliae* with *P. acaulis* and *P. elatior,* F_2 and backcross data were obtained; short styles were dominant over long, orange over yellow eye. In *P. vulgaris* one recessive gene is responsible for various defects in floral organs. A white-margined leaf type is recessive in *P. malacoides.* In *P. officinalis* a defective type with five extra pistils and no stamens is a simple recessive. Genetic analysis is most advanced in *P. sinensis,* in which 25 pairs of genes and 2 sets of

multiple allels are recognized. Fifteen of these genes have been located in four chromosomes. On selfing *P. kewensis*, a tetraploid species, and several types with respect to style length, fertility, greening in the corolla, and double-ness were obtained, but the parental types were not recovered. Other tetraploid forms which appeared in progenies of diploid *P. sinensis*, proved less fertile than the diploids. Only two of seven genes completely dominant in the diploid, proved completely dominant in the tetraploid, i. e., when one dominant gene and three recessives were opposed. A technical study of linkage in a tetraploid has been made.

Quamoclit. (Nohara, *395*.)

Two flower colors in *Quamoclit pennata* differ by a single gene, without dominance. Stem color may be determined by the same gene. The F_1 of *Q. coccinea* × *Q. pennata* is intermediate and sterile, although *Q. sloteri*, a fixed race, is believed to have arisen from such a cross.

Ranunculus. (Marsden-Jones and Turrill, *334;* Ragionieri, *422*.)

A double, large-flowered form is reported as the result of selection from *Ranunculus asiaticus*. Studies of inheritance of color, sex, and sterility in *R. acris* and *R. bulbosus* have not reached satisfactory analysis.

Reseda odorata L. (Compton, *80*.)

Orange-red pollen color appears to be a monogenic dominant to yellow, and self-compatibility has the same relation to self-incompatibility.

Rhododendron. (Ikeno, *230;* Miyazawa, *368*.)

In studies within the species *Rhododendron indicum* (*Azalea indica*) and in crosses of this species with *R. sinense*, single flowers were monogenically dominant to double, self-colored flowers to variegated, and short stamens to long. The prostrate habit is recessive to upright. Flower size and leaf breadth showed intermediate conditions in F_1. The hose-in-hose type in *R. indicum* var. *kaempferi* was interpreted as a dominant heterozygous form, the pure recessive being the normal type. The apetalous form (petals replaced by stamens) is a similar case but two genes are involved, the apetalous being heterozygous for both, and the normal type double recessive. "Polypetala" (petals separate instead of united) is a dominant heterozygous form, showing a single gene difference from normal.

Rosa. (Erlanson, *120;* Godfrey, *143;* Hurst, *225, 226*.)

Incompatibility and sterility present serious difficulties in rose breeding. Hurst and Erlanson have shown that extensive polyploid series occur in roses. Hurst found 377 diploids and 629 polyploids in 1,006 species and forms of *Rosa* examined. He considers that five diploid species fundamental to the genus have given rise to many other species in various polyploid combinations. The hybrid tea roses are chiefly tetraploids, and triploid forms also appear among garden hybrids. Pentaploid, hexaploid, and octoploid forms are also found in the genus.

Rudbeckia. (Blakeslee, *48*.)

Two forms with yellow disks were distinguishable by treatment with potassium hydroxide, one turning black, the other yellow. On crossing these two yellow types, purple (normal type) appeared in F_1, and in F_2, 9 purple : 3 "black-yellow" : 4 "red-yellow."

Salvia. (Bateson, Saunders, Punnett, and Hurst, *25;* Blaringhem, *52;* Hrubý, *219*.)

Pink flower color in *Salvia horminum* is a monogenic dominant to white, while violet is the result of interaction of the gene for pink with a second complementary gene which has no effect (i. e., white) when present alone. In the course of six generations of selfing of *S. pratensis* (normally hermaphrodite and blue-flowered), decreased vigor and fertility, and segregation of types with white flowers, female flowers, mosaic leaves, etc., were observed. Attempts to cross *S. nutans* with *S. juriscici* have thus far failed, but selfing of a supposed natural hybrid yielded parental types and an intermediate type like F_1.

Saponaria ocymoides L. (Meunissier, *344*.)

A large, pink-flowered type was found to be dominant to a small white type in F_1.

Saxifraga. (Marsden-Jones and Turrill, *335;* Whyte, *547*.)

Saxifraga potternensis is a tetraploid derivative of the cross *S. rosacea* × *granulata.* Its breeding behavior is uniform.

Senecio vulgaris L. (Trow, *515, 516, 517*.)

A scheme of at least 12 genes has been formulated to explain inheritance of a number of differences existing between various named types of this species.

The characters studied include type and color of heads, incision of rays, color of stems, color of leaves, number of nodes. Two or more instances of linkage are recognized.

Silene. (Correns, *91;* Marsden-Jones and Turrill, *336, 338;* De Vries, *528, 530.*)
Pigmented flowers in *Silene armeria* are dominant to white. On crossing white × rose flower color Correns found a monogenic relation, in which white and rose are pure breeding forms and the heterozygote is red. This red type was like the wild form in appearance, but the latter was found to be a pure-breeding red. *S. vulgaris* showed segregation for various characters on selfing. Segregation was noted also in the progeny of a cross of this species with *S. maritima.* A type with defective petals proved to be a simple recessive to normal.

Sisyrinchium angustifolium Mill. (Miyake and Imai, *352, 357.*)
On crossing a self-colored purple with a white with purple eye, a monogenic relation was found, the self-colored proving to be partially dominant.

Tagetes erecta L. (Punnett, *417.*)
The double flower is a monogenic dominant to single, and the flat type of floret to the tubular, the two characters showing independent inheritance. Two or more genes are apparently concerned in the difference between deep orange and lemon-yellow flower color.

Tetragonolobus purpureus Moench. (Nilsson, *391.*)
Yellow flower color is a monogenic recessive to red.

Tropaeolum majus L. (Correns, *98;* Eyster and Burpee, *125;* Rasmuson, *427, 432.*)
Monogenic differences were found between dark-yellow and light-yellow flowers, between red anthocyanin and its absence. Variegated flowers are dominant to self-colored. The climbing type is a monogenic dominant to the dwarf type. Dark-green leaf color is determined by two genes. Two defective types, pale green and white-spotted leaves, each proved to be simple recessives to normal green and showed independent inheritance. Doubleness and fragrance are monogenic recessives. "Super-double" is dominant to both single and common double.

Tropaeolum species hybrids. (Fischer, *129;* Warren, *535.*)
On crossing *Tropaeolum majus* × *T. minus*, red flower proved dominant to yellow, green leaf to variegated, and tall stature to dwarf. The gene for stature was partially linked with that for leaf color. In the hybrid between *T. minus* and *T. peregrinum*, known as *T. pinnatum*, red pigment in corolla and stem proved dominant to its absence, and the relation appeared to be monogenic.

Tulipa. (Hall, *190;* De Mol, *372.*)
So-called "thieves", narrow-petaled forms, are probably mutant forms in tulip varieties. They also occur in tulip bulbs X-rayed during flower formation.

Venidium × *Arctotis.* (Warren, *536, 537.*)
A natural hybrid, *Venedium wyleyi* × *Arctotis stoechadifolia* var. *grandis*, was largely intermediate between the parents but taller and bulkier. In F_2 no clear segregation occurred, but various characters showed dominance of one or the other parental types.

Verbascum blattaria L. (Shull, *473.*)
Bright yellow corolla is a monogenic dominant to pale yellow.

Verbascum phoeniceum L. (Sirks, *480, 483, 484.*)
The inheritance of self-compatibility and self-incompatibility in this species appears to be complex and somewhat irregular.

Verbena. (Eyster, *124.*)
Light variegations in flower color are dominant to heavy variegations; variegation is dominant to dilute self-color; light self-color is dominant to darker self-color.

Veronica gentianoides Vahl. (Correns, *98, 100.*)
The short-styled form is a heterozygous dominant, the long-styled is the homozygous recessive. Style length is further affected by a series of modifying genes. A white-margined form, on crossing with the normal, produced only normal in F_1 and F_2, the defective type showing no genic inheritance.

Veronica longifolia L. (De Vries, *528, 530.*)
The white-flowered type is recessive to the pigmented form, the recessive occasionally appearing as a somatic mutation in large F_1 populations.

Veronica syriaca Roem. and Schult. (Filzer, *128;* Lehmann, *315, 316, 317, 318.*)
Blue flowers are monogenically dominant to rose and white. Self-sterility is determined by a series of multiple allels, which accelerate or inhibit pollen-

tube growth in compatible and incompatible styles. In the F_2 of a cross, four intrasterile but interfertile groups appeared.

Veronica tourneforti C. C. Gmel. (Beatus, *41.*)

In this tetraploid species, number of sepals (four or five) appears to be determined by a series of multiple allels.

Viola arvensis Murray. (Clausen, *72.*)

Study of inheritance of a spot on the style revealed unusual relations, which were explained on the assumption of three or more pairs of genes.

Viola tricolor L. (Clausen, *72, 73, 74;* Kristofferson, *303, 305.*)

The inheritance of flower color is somewhat complex, indicating gene interactions. The presence of a colored spot on the front of the style is dominant to its absence. A second type of spot requires the presence of another gene before it can appear. The prostrate habit of growth in the variety *maritima* is dominant to the erect type of other varieties. Some characters, such as variegations, are apparently non-Mendelian. They appear to depend on plastids in the cytoplasm. The velvety black flower color of *Viola tricolor* var. *nigra* is reported to be determined by three basic genes for expression of color, and five inhibitor genes, which suppress the development of velvety black.

Viola species hybrids. (Clausen, *75.*)

Clausen has reported 25 successful species crosses. *Viola tricolor* and *V. arvensis* cross with many species; *V. cornuta* with only *V. orphanoides* and *V. elegantula; V. calcarata* with only *V. battandieri.* Some new fertile types have been isolated from crosses.

Zantedeschia (Richardia). (Ragionieri, *421.*)

In a cross between *Zantedeschia rehmannii* and *Z. elliottiana* most of the characters of the latter proved dominant in F_1, the yellow spathe color being an exception. In F_2 spathe color, size, form, spotting of leaves, etc., showed segregation, but the number in the progenies were too small for interpretation of genic relations.